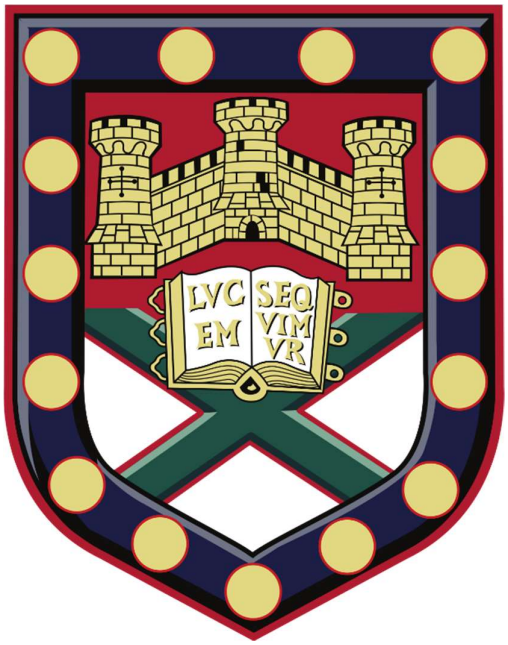
Exploring the relationship between spatial cognitive ability and movement ecology



Submitted by Christine Elizabeth Beardsworth to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Psychology

October 2019

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature: ……

Abstract

Spatial cognitive ability is hypothesised to be a key determinant of animal movement patterns. However, empirical demonstrations linking intra-individual variations in spatial cognitive ability with movement ecology are rare. I reared ~200 simultaneously hatched pheasant chicks per year over three years in standardised conditions without parents, controlling for the confounding effects of experience, maternal influences and age. I tested the chicks on spatial cognitive tasks from three weeks old to obtain measures of inherent, early-life spatial cognitive ability. Each year, I released birds when 10 weeks old into an open-topped enclosure in woodland. Birds dispersed from this enclosure after about one-month. Importantly, all birds were released into the same, novel area simultaneously, thus their experiences and opportunities were standardised. I remotely tracked pheasant movement through either RFID antenna placed under 43 supplementary feeders situated throughout our field site (2016) or by using a novel reverse-GPS tracking system (2017-2018). Spatial cognitive ability, determined through binary spatial discrimination (2016) or a Barnes maze (2017), was related to the diversity of foraging sites an individual used (**Chapter 2**: 2016). Those with better spatial cognitive ability used a more diverse range of artificial feeders than poor performing counterparts, perhaps to retain a buffer of alternative foraging sites where resource profitability was known. I found no relationship between the timing of daily foraging onset between birds of differing cognitive ability (**Chapter 3**; 2016), which I had hypothesised to be a consequence of birds developing efficient routes between refuges and feeders. After establishing a reverse GPS system on our field site (**Chapter 4:** 2017), I collected more detailed information about pheasant movement and found that birds with higher accuracy scores on the cognition tasks initially moved between

foraging and resting sites more slowly than inaccurate birds in novel environments, perhaps to gather more detailed information. Accurate birds increased their speed over one month to match the same speed as inaccurate birds. All birds increased the straightness of their routes at a similar rate. Lastly, I found intraspecific differences in the orientation strategy that birds used to solve a dual strategy maze task (**Chapter 5**: 2018). These differences predicted habitat use after release: birds that utilised landmarks (allocentric strategies) showed less aversion to urban habitats (farm buildings/yards) than egocentric/mixed strategy birds, which is potentially due to the presence of large, stable landmarks within these habitats. In this thesis, I provide several empirical links between spatial cognitive ability and movement ecology across a range of ecological contexts. I suggest that very specific cognitive processes may govern particular movement behaviours and that there is not one overarching general spatial ability.

Acknowledgements

This project was part of a wider group effort and would frankly not have been possible without the support of the other members of the Pheasant Ecology and Cognition research group. Joah, your ambition for this project was extraordinary and your attitude throughout my PhD has been inspiring. Despite numerous problems with technology, suppliers and the local wildlife consuming our study system, you have remained calm, supportive and decisive throughout. You are a brilliant, forward thinking, optimistic and inspirational supervisor, who gave me an opportunity that I will be forever grateful for.

Mark, your commitment to the PhD students in the group is phenomenal and I have been really lucky to work with you. You are always willing to help out and you have taught me so much about fieldwork. Thank you for checking up on me while I have been a writing-up hermit.

During the course of this project, I have worked with a wonderful set of research assistants and master's students. Molly Watts and Heather Warrender assisted in 2016. Molly's sensational cooking combined with Heather's hilarious character made for a happy first field season, despite nostalgic claims from the others that 'the first [previous] season was the best'. It wasn't. Kenzie, my game of thrones buddy, your riddles were immense and we weren't able to recreate your unique style of delivery in any subsequent field seasons. Other field assistants joined us over the next few years: Joe, Camille, Josh, Elena, Kandace and Anna; thank you for all your help.

Clearly, the core PEC group need a massive thank you. Jayden, thank you for your frequent reminders that there is life outside of academia. Ellis, you have been an inspiration from the beginning, only 6 months ahead of me in your PhD yet you are so wise! You are detail-oriented, thoughtful and I am glad we shared this experience together. Pip, BP was rubbish. I'm so grateful to have you around to bounce ideas off, calm me down and generally be an awesome friend. Lucy, the honorary pheasant ecologist, thank you for always being available to go to the pub, being my spatial analysis friend and fellow Northerner.

The wider CRAB lab have played a critical role in my development as a researcher, giving feedback on talks, help with statistical analysis and advice on academia. In particular, Andy Higginson, you helped me to see the bigger picture and your advice has been invaluable. Tim and Lisa, thank you for your help in attaining my teaching qualification and for giving me constructive feedback. Rob, your enthusiasm for research is contagious, thank you for undergoing the 'ATLAS experience' with me. Mike, you were always willing to help with my statistical queries and be optimistic about my work when I felt it wasn't going anywhere. Katie, thank you for making me laugh, everyone needs a Katie. Chloe and Sylvia, the dream team. Thank you for your encouragement over the years. I am so glad you were around to show me the ropes and if it didn't include writing a thesis, I would say let's do it all again!

Amy, you have been there for me every step of the way, despite living in a different country for most of it. Our skype calls and gaming sessions kept me sane and I can't imagine doing this without you. Emma, by teaching me how to use QGIS, you have played a pivotal role in the development of three chapters. Your helpful nature has been vital in the final stages and I can't thank you enough for being there whenever needed.

To my family. Mum, I know you are proud, whatever it is you think I actually do. At least now, you can forward family members this document instead of trying to explain why I teach pheasants how to solve mazes. Dad, thank you also for your support in all aspects of life, I don't know what I would do without you. I love you both.

Gill, my soon-to-be mother-in-law, you are bonkers, and I wouldn't have it any other way. I am glad I will finally be able to answer the question 'when will you finish your PhD?'. Tony, you supported me through everything. You were a wonderful man who is dearly missed. I wish we could have one last chat.

Finally, Matt. You upturned your life to move to Exeter with me. You have supported me in every way throughout this degree, despite me ditching you every summer to go and live with pheasants. I could not have completed it without you and I love you.

Declaration

Thesis Chapters

This thesis comprises five data chapters, each of which is written as a manuscript for submission for publication and is intended to stand alone. While the candidate is the primary contributor to all chapters, significant contributions from co-authors are reflected by using the plural 'we' where the first-person is used. Three supervisors provided comments on drafts of the thesis: Dr Joah Madden provided comments on drafts from all Chapters, Dr Mark Whiteside provided comments on Chapters 2,3,5,6 and 7 and Dr Andrew Higginson provided comments on Chapter 5. All data was collected during the PhD period. Contributions of co-authors to each chapter is declared below.

Chapter Two: Individual differences in spatial cognitive ability predicts the use of multiple foraging sites in an enclosed but natural habitat

CE Beardsworth, EJG Langley, MA Whiteside, JO van Horik, JR Madden

CEB and JRM conceived the idea; CEB conducted the analyses and wrote the chapter; CEB, EJGL, MAW, JOvH and JRM collected the data and provided comments on the draft.

Chapter Three: Daily patterns of foraging onset are repeatable and have survival implications but are driven by non-cognitive not cognitive factors

CE Beardsworth, EJG Langley, MA Whiteside, JO van Horik, JR Madden

CEB and JRM conceived the idea; CEB conducted the analyses and wrote the chapter; CEB, EJGL, MAW, JOvH and JRM collected the data and MAW, EJGL and MAW provided comments on the draft.

Chapter Four: Coverage, accuracy and precision of a novel Reverse-GPS animal tracking system in a hilly and heterogenous environment

CE Beardsworth, JR Madden

CEB and JRM conceived the idea; CEB collected the data, conducted the analyses and wrote the chapter; JRM provided comments on the drafts.

Chapter Five: The speed and straightness of transitory paths in young birds released to a novel environment relates to accuracy in a spatial cognition task

CE Beardsworth, LA Capstick, PR Laker, EJG Langley, R Nathan, Y Orchan, S Toledo, JO van Horik, MA Whiteside, JR Madden

CEB and JRM conceived the idea; CEB conducted the analyses and wrote the chapter; CEB, LAC, PRL, EJGL, MAW, JOvH and JRM collected the cognition data, CEB, MAW, JRM collected the movement data. RN, YO and ST developed the reverse-GPS system and provided support throughout data collection.

Chapter Six: Individual orientation strategies shape habitat preferences in the wild

CE Beardsworth, PR Laker, R Nathan, Y Orchan, S Toledo, JO van Horik, MA Whiteside, JR Madden

CEB and JRM conceived the idea; CEB conducted the analysis and wrote the chapter; CEB, PRL, MAW, JOvH and JRM collected the cognition data, CEB, MAW, JRM collected the movement data. RN, YO and ST developed the reverse-GPS system and provided support throughout data collection.

Co-authored papers

During the data collection for her own work, the candidate assisted in data collection for other projects with other members of the lab. This has led to the publication of 13 co-authored papers which are detailed below:

2020

EJG Langley, G Adams, **CE Beardsworth**, DA Dawson, PR Laker, JO van Horik, MA Whiteside, AJ Wilson, JR Madden. Heritability and correlations among learning and inhibitory control traits. *Behavioral Ecology*, 1–9. https://doi.org/10.1093/beheco/araa029

EJG Langley, JO van Horik, MA Whiteside, **CE Beardsworth**, MN Weiss, PR Laker, JR Madden. Early life learning ability predicts adult social structure, with potential implications for fitness outcomes in the wild. *Journal of Animal Ecology*, 1365-2656.13194. https://doi.org/10.1111/1365-2656.13194

KR Griffin, **CE Beardsworth**, PR Laker, JO van Horik, MA Whiteside, JR Madden. The inhibitory control of pheasants (Phasianus colchicus) weakens when previously learned environmental information becomes unpredictable. *Animal Cognition* 23, 189-202

JO van Horik, **CE Beardsworth**, PR Laker, EJG Langley, MA Whiteside, JR Madden Response learning confounds assays of inhibitory control on detour tasks. *Animal Cognition* 23, 215-225 https://doi.org/10.1007/s10071-019-01330-w

2019

JO van Horik, **CE Beardsworth**, PR Laker, EJG Langley, MA Whiteside & JR Madden (2019) Unpredictable environments enhance inhibitory control in pheasants. *Animal Cognition,* https://doi.org/10.1007/s10071-019-01302-0

MA Whiteside, JO Van Horik, EJG Langley, **CE Beardsworth**, LA Capstick & JR Madden (2019) Patterns of association at feeder stations for Common Pheasants released into the wild: sexual segregation by space and time. *Ibis*, 161 (2), 325-336. https://doi.org/10.1111/ibi.12632

2018

JR Madden, EJG Langley, MA Whiteside, **CE Beardsworth** & JO van Horik (2018) The quick are the dead: pheasants that are slow to reverse a learned association survive for longer in the wild. *Philosophical Transactions B*, 373 (1756), 20170297. https://doi.org/10.1098/rstb.2017.0297

JO van Horik, EJG Langley, MA Whiteside, PR Laker, **CE Beardsworth** & JR Madden (2018) Do detour tasks provide accurate assays of inhibitory control? *Proceedings of the Royal Society B: Biological Sciences*, 285: 20180150. https://doi.org/10.1098/rspb.2018.0150

JO van Horik, ELG Langley, MA Whiteside, **CE Beardsworth**, JR Madden (2018) Pheasants learn five different binomial colour discriminations and retain these associations for at least 27 days. *Animal Behaviour and Cognition*, 5(3), 268-278. https://doi.org/10.26451/abc.05.03.02.2018

EJG Langley, JO van Horik, MA Whiteside, **CE Beardsworth** & JR Madden The relationship between social rank and spatial learning in pheasants, *Phasianus colchicus*: cause or consequence? (2018) *PeerJ 6:*e5738 https://doi.org/10.7717/peerj.5738

MA Whiteside, JO van Horik, EJG Langley, **CE Beardsworth** & JR Madden (2018) Size Dimorphism and sexual segregation in pheasants: tests of three competing hypotheses. *PeerJ,* 6. e5674 https://doi.org/10.7717/peerj.5674

MA Whiteside, MM Bess, E Frasnelli, **CE Beardsworth**, EJG Langley, JO van Horik & JR Madden (2018) Low survival of strongly footed pheasants may explain constraints on lateralization. *Scientific Reports*, 8 (13791), https://doi.org/10.1038/s41598-018-32066-1

2017

MA Whiteside, JO van Horik, EJG Langley, **CE Beardsworth**, PR Laker & JR Madden (2017) Differences in social preference between the sexes during ontogeny drive segregation in a precocial species*. Behavioral Ecology and Sociobiology*, 71 (7), 103. https://doi.org/10.1007/s00265-017-2332-2

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1 General Introduction

1.1 Introduction

Movement is a fundamental behaviour for many species, allowing an animal to find food, mates and avoid predation. The mechanistic basis underlying movement decisions has had much theoretical attention (Benhamou, 2014; Fagan et al., 2013; Mueller, Fagan, & Grimm, 2011; Van Moorter et al., 2009) and a holistic approach to understanding how, why and when animals move has been suggested (Nathan et al., 2008). Information about internal (e.g. nutritional, endocrinological or immunological (Jachowski & Singh, 2015)) and external factors (e.g. resource distribution (Reyna-Hurtado et al., 2018), predation risk (Creel, Winnie, Maxwell, Hamlin, & Creel, 2005; Fraser, Gilliam, Albanese, & Snider, 2006) or social influences (Polansky, Kilian, & Wittemyer, 2015; Strandburg-Peshkin, Farine, Couzin, & Crofoot, 2015)) feed into cognitive processes that aid an animal in making effective decisions. Despite the importance of cognition, the ability to collect, process, store and utilise information (Shettleworth, 2010), only 1.6 % of movement ecology studies have focussed on cognitive underpinnings of movement (Joo et al., 2019). Remembering important locations can influence the use of the spatial environment, for example, by biasing movement towards profitable locations such as foraging sites (Bracis, Gurarie, Van Moorter, & Goodwin, 2015). Memory has been demonstrated to influence patterns of movement from the large scale migration patterns of blue whales, *Balaenoptera musculus* (Abrahms et al., 2019) to the daily foraging routes of bumble bees, *Bombus terrestris* (Osborne et al., 2013). Movement itself can have fitness consequences, which can shape distributions and population growth rates (Alves et al., 2013). In turn this likely exerts selection pressures on underpinning cognitive processes.

Individuals differ in their cognitive ability (Thornton & Lukas, 2012). Critically, even subtle differences in the acquisition of information (learning) and recall and use of that information (memory) can affect the behaviour of individuals. For instance, bumble bees that learn about their environment quicker have been demonstrated to be better foragers (Raine & Chittka, 2008) and more accurate memory can help individuals to avoid specific areas of high predation risk which may help survival (Ings & Chittka, 2008). Individual differences in cognitive abilities are an important component in explaining ecological processes (Thornton & Lukas, 2012) and have been shown to be related to fitness proxies such as survival (Maille & Schradin, 2016a; Sonnenberg, Branch, Pitera, Bridge, & Pravosudov, 2019; Whiteside, Sage, & Madden, 2016), mating success (Shohet & Watt, 2009; Smith, Phillips, & Reichard, 2005) and reproductive investment (Branch, Pitera, Kozlovsky, Bridge, & Pravosudov, 2019; Shaw, MacKinlay, Clayton, & Burns, 2019).

Explicit links between cognitive ability and spatial ecology in the real world are rare. Typically, such approaches have involved testing individuals using classical psychometric tests developed in comparative psychology (e.g. Olton and Samuelson 1976) to assess the ability of an animal to learn and remember spatial information, and relating this to some aspect of their movement and space use. Previous work has usually compared distinct natural or experimental groups that differ in natural space. For instance, male meadow voles, *Microtus pennsylvanicus* perform better on spatial cognitive tasks than females (Gaulin & Fitzgerald, 1986, 1989; Jacobs, Gaulin, Sherry, & Hoffman, 1990; Sherry, Jacobs, & Gaulin, 1992). This difference was suggested to be linked to distinct differences in spatial ecology between the sexes, with male meadow voles

maintaining larger home ranges than females. Other studies have found similar links between spatial ability in habitat complexity (Lucon-Xiccato & Bisazza, 2017) and breeding behaviours (Astié, Kacelnik, & Reboreda, 1998; Guigueno, Snow, MacDougall-Shackleton, & Sherry, 2014), where sexes differ in their use of the spatial environment, demonstrating a clear link between spatial ability and space use. While these studies have been crucial to establishing the importance of spatial cognition in real-world environments, the extent to which variation in spatial ability at the individual level influences movement and space use has largely been ignored. Yet, even within the sexes, distinct differences in movement behaviour have been linked to performance in spatial cognitive tasks. For example, male domestic chickens *Gallus gallus domesticus* that utilise more space in their enclosure have better scores on spatial tasks (Bessa Ferreira et al., 2019; Campbell, Talk, Loh, Dyall, & Lee, 2018). Shaw *et al*. (2019) found that male New Zealand robins, *Petroica longipes,* with better spatial memory spent less time flying while foraging and provisioning their offspring, as well as providing a higher proportion of large food items to chicks in the nest, thus limiting costly movements and maximising the efficiency of foraging trips.

The limited number of studies that attempt to assess how variation in cognitive traits influence real-world movement behaviour is unsurprising. To begin to answer questions about this relationship, a number of criteria must be met. First, accurate and robust assays of individual cognitive performance should be established (**Section 1.2**). After cognitive ability has been assessed, accurate measures of movement, and/or space use are required to measure natural behaviours in a real-world environment (**Section 1.3**). I outline scenarios in which spatial cognition has previously been suggested to link to movement ecology

(**Section 1.4**), before making specific predictions to outline the scope of this thesis (**Section 1.5**). Finally, I discuss the requirements of a study system for testing these predictions (**Section 1.6**) and describe how the pheasant, *Phasianus colchicus,* provides a unique and useful model system (**Section 1.7**).

1.2 Spatial Cognition and Navigation in Animals

1.2.1 What is cognition?

The term 'cognition' is surprisingly controversial, with little agreement on the exact meaning of the terminology (Bayne et al., 2019). In this thesis, I will use the term cognition to describe the mechanisms by which animals collect, process, store and act upon information from the environment, including perception, learning, memory and decision-making (Shettleworth, 2010). Environmental cues provide information that an animal can act upon and the type of information that an animal uses are often determined by the ecology of the species (Stevens, 2013). For instance, caching species rely heavily on remembering the spatial location of their caches to survive winter periods (Pravosudov & Roth II, 2013). This dependence on spatial information has been demonstrated to be linked to an increased ability to remember spatial cues, when compared to non-caching species (Healy, Clayton, & Krebs, 1994), yet the ability to remember other types of information, for instance colour cues, is not extraordinary in caching species (Olson, Kamil, Balda, & Nims, 1995).

Once an animal has collected information, they can store it in two types of memory. Short-term memories can be created moment-to-moment and are stored in working memory, where they are forgotten soon after. This is useful to

remember things that will be irrelevant shortly after. Alternatively, information can be stored in reference memory and can be accessed for days or years after learning (Dukas, 1998). However, storing information unnecessarily is likely to be costly. Neurological costs of memory formation, seem to trade-off with other mechanisms that influence fitness (Aiello & Wheeler, 1995). For example, *Drosophila melanogaster* that have been selected for improved learning ability demonstrate a decline in larval competitive ability (Mery & Kawecki, 2003). Therefore, only relevant and useful information should be stored.

There are two main contrasting and highly debated theories for the organisation of cognitive processes. First, the domain-specific view of cognition suggests that cognition is organised in a modular way, allowing different domains to become specialised independently (Shettleworth, 2012). In contrast the domain-general view suggests that cognitive abilities are underpinned by a general cognitive or intelligence factor (*g*) (Duncan et al., 2000). Both theories suppose that performance on tasks that target the same 'domain' are correlated. Spatial cognition is a 'domain' of cognitive processes and is often used as an overarching term that describes the ability to learn locations, routes and/or geometric relationships between objects (Colby, 2009). Spatial cognitive ability, a term that is frequently used in this thesis, describes an animal's ability to use spatial information to complete behavioural tasks, generally relative to other individuals. This can be evaluated through assessing learning (acquisition) or memory (retention) of spatial cues in behavioural tasks (see Section 1.2.4), where spatial location predicts reward. These scores provide a means to compare performance between individuals (Balda & Kamil, 1988b; Clayton & Krebs, 1994b; Galea, Kavaliers, & Ossenkopp, 1996). It is important to note that while other domains

have received attention in assessing within-domain consistency in individuals for particular tasks (e.g. colour associative learning van Horik, Langley, Whiteside, & Madden, 2018), within the spatial domain there is little evidence to suggest that there is one easily identifiable and overarching 'general' spatial ability, whereby performance of any task where spatial information predicts reward would converge on similar results across contexts. Care should therefore be taken in the interpretation of results when performance in a single task is found to be related particular behavioural phenomenon (e.g. White, Wagner, Gowan, & Braithwaite, 2017).

1.2.2 How do animals navigate?

Animals can use a variety of strategies to aid their navigation (see Table 1.1 for a summary of common strategies). Many animals use path integration as a

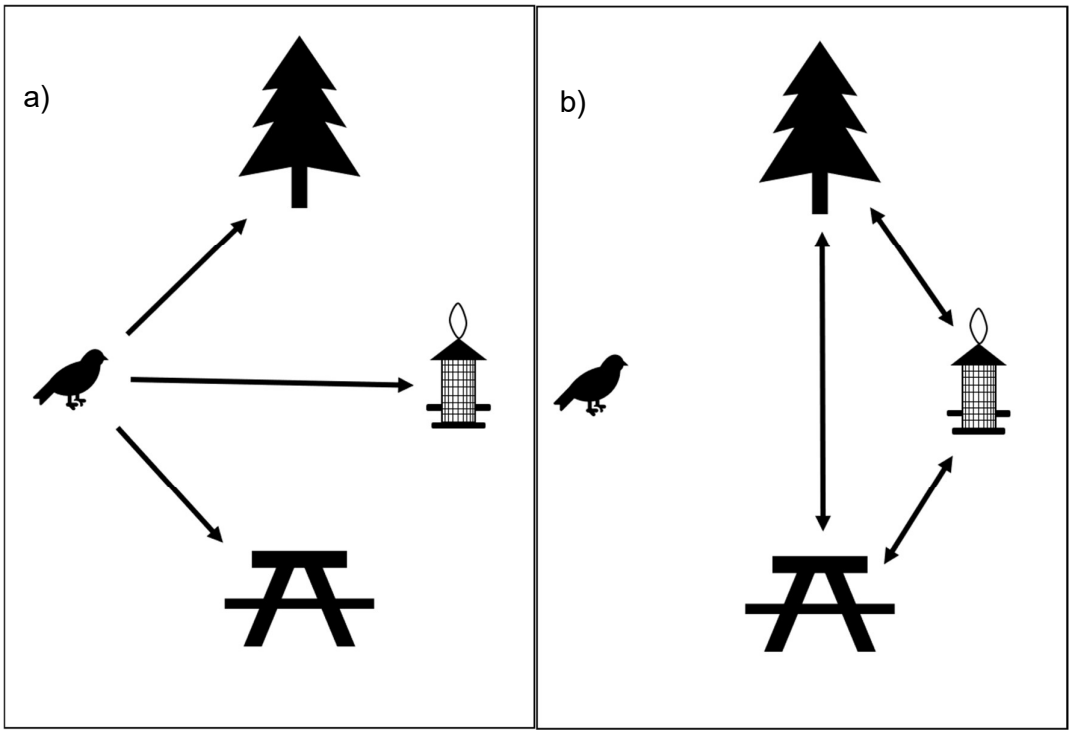


Figure 1.1 a) Perception of locations relative to the observer – Egocentric orientation b) Perception of locations relative to other landmarks – Allocentric orientation

fundamental method of navigation by continuously updating their internal record of direction and distance travelled from their starting point (Benhamou, 1997; Collett & Collett, 2000; Mittelstaedt & Mittelstaedt, 1980). However, errors can quickly accumulate using path integration alone (Benhamou, Sauvé, & Bovet, 1990; Heinze, Narendra, & Cheung, 2018). For many species, path integration provides a scaffold for view-based learning, allowing individuals to encode the location of landmarks along a route, segmenting each vector so that accuracy is increased (Müller & Wehner, 2010).

As experience of an environment increases, memory can increase the efficiency of navigation (Collett & Collett, 2002) and enable animals to relocate to important features of the environment such as foraging patches, safe sleeping sites, water sources or potentially risky areas (Fagan et al., 2013). Locations can be encoded relative to the observer (egocentric) allowing mice to relocate their nest site in complete darkness (Mittelstaedt & Mittelstaedt 1980). Alternatively, locations can be encoded relative to other external features (allocentric) such as landmarks or snapshot views of surrounding features (Figure 1.1; Burgess, 2006; O'Keefe & Nadel, 1978). For example, young honeybees, *Apis melifera* will perform a series of 'orientation' flights over subsequent days to view the hive from different viewpoints and learn features of the local landscape before becoming a forager, ensuring that the location of the hive is known from all directions (Capaldi et al., 2000; Menzel, De Marco, & Greggers, 2006). These orientation mechanisms can be used in isolation or in combination with one another, which can often depend on the salience of external cues.

1.2.3 Neural mechanisms of spatial cognition

In vertebrate species, the hippocampus is particularly important for spatial representation in the brain and differences in the structure of the hippocampus has been linked to differences in ecological challenges. For instance, caching species have a larger hippocampal volume than non-caching species (Healy et al., 1994; Healy & Krebs, 1992). This is also the case within-species, where differences in the spatial ecology of the sexes lead to increased demands on spatial memory in one particular sex (e.g. brown-headed cowbirds *Molothrus ater* (Sherry, Forbest, Khurgel, & Ivy, 1993), meadow voles, *Microtus pennsylvanicus* (Jacobs et al., 1990)) or different populations (Roth & Pravosudov, 2009). While much of the focus of cellular and circuit mechanisms of spatial representation centre on the hippocampal and parahippocampal formation, a variety of other neuronal mechanisms are involved in an animal's spatial decisions, movement and navigation, engaging a wide array of brain circuitry (for reviews: Moser, Kropff, & Moser, 2008; Moser, Moser, & McNaughton, 2017). Egocentric and allocentric orientation systems are suggested to be neuronally distinct in mammals (Aagten-Murphy & Bays, 2019; McDonald & White, 1994), birds (Fremouw, Jackson-Smith, & Kesner, 1997; Shimizu, Bowers, Budzynski, Kahn, & Bingman, 2004) and fish (Broglio, Rodríguez, & Salas, 2003; López, Broglio, Rodríguez, Thinus-Blanc, & Salas, 1999), allowing both allocentric and egocentric strategies to be used either independently or in conjunction with one another. Information about spatial cues used in allocentric orientation are primarily stored in the hippocampus (Fremouw et al., 1997; O'Keefe & Nadel, 1978), while the striatum plays a pivotal role in the processing of egocentric cues (Burgess, 2008) but other brain regions can also play a role (Moser et al., 2008).

Table 1.1 Summary of common explanations for movement behaviour (Modified from Gould & Gould, 2012b).

Strategy	Description	Example
Taxis	Orienting directly towards or away from a cue.	Male moths searching for a mate move towards more concentrated areas of the pheromone produced by females (chemotaxis) (Farkas & Shorey, 1972).
Compass Orientation	Maintaining a constant bearing relative to a cue, or a constant absolute direction if compensating for cue movement. Types of compass systems involve the sun, starts, polarized light and magnetic field compasses.	Sea turtles make transoceanic migrations using the earth's magnetic field for both longitude and latitude (Lohmann, 2007).
Path integration	Also known as dead reckoning or inertial navigation. Keeping track of directions and distances from some reference point on one or more legs of a journey to compute location.	Desert ants navigate long distances using sensory cues such as wind and light, to monitor the direction of movement (Müller & Wehner, 2006, 2007) and through self-monitoring the distance travelled through step-integrators (Wittlinger, Wehner, & Wolf, 2006).
Piloting	Navigating a route relative to familiar landmarks.	Brown surgeonfish, *Acanthurus nigrofuscus*, follow a series of landmarks on daily 1.5km migrations to foraging sites (Mazeroll & Montgomery, 1998). These paths are diverted when landmarks are displaced.

1.2.4 Methods for studying spatial cognition

Cognitive processes themselves cannot be directly measured (Völter, Tinklenberg, Call, & Seed, 2018) and in non-human animals, a lack of verbal communication makes it particularly difficult to obtain information about these processes. Therefore, we can most simply adjudicate an animal's cognitive processes by observing behavioural changes that results from decisions made based on information that has been learned and remembered. This behavioural approach has underpinned a large literature of comparative psychology (for a review see Paul et al. 2009) in which researchers have adapted psychometric tasks to obtain behavioural proxies for cognitive processes. Through utilising different tasks and assessing behavioural responses, researchers can obtain information about an individual's learning speed (Brust & Guenther, 2017; Ings & Chittka, 2008; Sewall, Soha, Peters, & Nowicki, 2013), accuracy of memory (Balda & Kamil, 1988a; Barkley & Jacobs, 2007; Whiteside, Sage, et al., 2016), duration of memory (Smulders, Gould, & Leaver, 2010), working memory (or short term memory) performance (Spetch & Edwards, 1986; Harker & Whishaw, 2002) or a general performance measure (Langley, van Horik, Whiteside, & Madden, 2018b).

Perhaps the simplest test of spatial cognitive ability are binary choice tasks. Tasks such as the T-maze or the Y-maze consist of a 3-arm maze whereby the animal will enter the maze through one arm. A choice must then be made to turn left or right, allowing for simple spatial learning tasks to be conducted on a range of species (Japanese quail *Coturnix japonica* (Marin, Satterlee, Cadd, & Jones, 2002), cuttlefish (Jozet-Alves, Modéran, & Dickel, 2008), grey bamboo sharks,

Chiloscyllium griseum (Schluessel & Bleckmann, 2012), cockroaches, *Periplaneta americana* (Barraco, Lovell, & Eisenstein, 1981)).

More complex tasks offer the opportunity to probe different memory processes. For instance the radial arm maze (Olton & Samuelson, 1976) consists of multiple arms radiating from a central platform. At the end of each arm is a food reward that cannot be seen from the centre of the maze. Individuals must visit each arm to retrieve all of the rewards and revisits to arms where the reward has already been taken are counted as errors. This particular method is a good indicator of working memory, as the animal must remember where it has already recently removed the reward (Olton & Samuelson, 1976). By baiting only specific arm(s), experimenters can also assess spatial reference memory by counting entries into incorrect arms as errors. However, the use of classic radial arm mazes can require extensive training in some species (Moore & Osadchuk, 1982) and therefore may only be suitable for use with certain systems. This can be prohibitive but can be overcome by adapting the protocol to involve an open maze with no corridors, such as the Barnes maze (Barnes, 1979) (e.g. Pigeons *(Columba livia)* Balda & Kamil, 1988; Clark's nutcrackers *(Nucifraga columbiana)* Spetch & Edwards, 1986). This analogue to the radial arm maze has been very successful in assessing spatial reference memory in wild birds (Croston et al., 2016; Sulikowski & Burke, 2011).

Foraging grids, whereby food rewards are stored in hidden locations, provide a useful alternative to maze tasks, suitable for many species and which can be adapted to spatial ability in the wild (Ashton, Ridley, Edwards, & Thornton, 2018;

Pravosudov, Lavenex, & Omanska, 2005), as well as in the laboratory (Sutherland & Gass, 1995). Foraging grids are especially well suited to testing the memory of caching species as they closely mimic a strategy that caching species readily use in the wild. For instance, Pravosudov et al. (2005) allowed western scrub-jays (*Aphelocoma californica*) to cache food and then counted the number of searches to retrieve the food after a retention interval of 1 or 10 days. However, these studies can also be adapted for use with non-caching species by allowing them to search for a reward hidden by the experimenter in the same place over multiple trials (Ashton et al., 2018; Sewall et al., 2013; Shaw, Boogert, Clayton, & Burns, 2015a). The number of searches in unrewarded locations (errors) and the decrease in the number of errors over multiple trials, can be compared among individuals to assess spatial ability. This paradigm can be simplified with choices reduced to a binary pair of foraging locations (1 x 2 array) providing a basic test of learning about positional information (Langley, van Horik, Whiteside, & Madden, 2018b).

Many studies assay spatial cognitive ability with only one of these common tasks (e.g. Tierney and Andrews 2013; Croston et al. 2016), yet behaviour of free roaming individuals could be driven by highly specific spatial cognitive processes that may not be detected by any single task or may only be detected by a highly specific task. Few studies have investigated contextual repeatability in performances across tasks aimed at assessing the same putative domain, but it is indicated to be low ($R = 0.28$, Cauchoix et al. 2018) demonstrating the importance of conducting multiple assays of similar tasks. Furthermore, apparently similar tasks administered at different scales may measure very different cognitive processes (Guigueno, Macdougall-Shackleton, & Sherry,

2015). Even when the same task is used, individuals may utilise the spatial cues available in different ways (egocentric or allocentric) (Sauce et al., 2018) or differ in their attention according to the salience of these cues (Marchette, Bakker, & Shelton, 2011). This means that obtaining robust measures of an individual's performance across repeated cognitive tests is not trivial.

1.2.5 Concluding comments

Spatial cognition can be assessed through behavioural proxies, namely performance on a range of psychometric tasks (Paul et al., 2009), thus giving a measure for spatial cognitive ability that can be compared between individuals. However, the precise cognitive processes that are measured by each task may differ, even though all tasks were designed to assess spatial cognition. It is therefore importance to choose tasks that are suitable to the species, system and critically, to the questions being asked. Furthermore, testing contextual repeatability between tasks may help to identify to specific cognitive processes underlying performances in the tasks.

1.3 Measuring movement in free-roaming animals

Movement can be studied through two fundamental approaches. Firstly, the Eulerian approach considers animal movement by monitoring presence at fixed spatial locations (Turchin, 1998). For example, migration patterns have been monitored for decades through observations of marked individuals arriving at sites of interest such as breeding, moulting or over-wintering sites. However, monitoring individual movement through traditional observation techniques, such as recording coloured leg bands, can be time intensive and can sometimes

require the participation of thousands of volunteer observers. Despite this effort, misidentification of faded colour rings, codes or even duplication of sequences among countries and differences in detectability between sites according to their habitat can cause problems for the accuracy of studies (Sanders, 2017). In contrast, Lagrangian studies focus on moving individuals (Turchin, 1998). For instance, logging individual animals' locations at discrete time points, regardless of where they are in space. The advance of remote sensing technology can help us to understand the behaviour of free-ranging animals whilst undisturbed by humans in their natural environment (Cooke et al., 2004). In the following section I will explore some of the technology available to monitor animal movement.

1.3.1 Eulerian methods

1.3.1.1 Camera Traps

Motion-activated cameras (aka camera traps) have been shown to be a highly effective method of monitoring movement and activity. Although camera trapping has been used to monitor animals since the late 1920's (Chapman, 1927), only recently have camera traps been relatively affordable, yielding a non-invasive, easily deployed and robust option to suit a majority of terrestrial study species. Individuals can be identified on timestamped digital photographs, either through unambiguous features such as coat patterns (Karanth, 1995), or by capturing and marking/tagging the animals before the study begins (Brides, Middleton, Leighton, & Grogan, 2018). Networks of camera traps have proven to be effective in monitoring elusive and cryptic species (Karanth, 1995; Linkie et al., 2013), group demographics and dynamics (McCarthy et al., 2018), home range size (Gil-Sánchez et al., 2011) and habitat use (Bowkett, Rovero, & Marshall, 2008). However, this approach results in the production of thousands (sometimes

millions) of both useful and useless images that require classification. Methods of reducing the workload for researchers include using citizen scientists to classify images (Swanson, Kosmala, Lintott, & Packer, 2016) or complex machine learning algorithms (Gomez Villa, Salazar, & Vargas, 2017), although the latter still requires a significant number of training images to be verified, before the resulting model can be tested and used.

1.3.1.2 RFID

Radio-frequency identification (RFID) combined with Passive Integrated Transponder (PIT) tags provides an automated alternative to camera trapping and has also become popular with ecologists in recent years (Farine, Aplin, Garroway, Mann, & Sheldon, 2014; Nomano, Browning, Nakagawa, Griffith, & Russell, 2014; Schulte & Steinfartz, 2007). PIT tags are relatively inexpensive and their low-cost enables researchers to tag entire populations and study community level ecology (Cooke et al., 2013). Tags can be either inserted subcutaneously into the animal or can be worn e.g. as a collar or leg ring. They emit a weak signal when activated by a more powerful transmitter (RFID receiver) at short range. These signals are unique to each tag and therefore allow for automatic and accurate detection of any tagged individual in the vicinity of an RFID reader. PIT tags themselves do not require a battery (although the receiver must be powered) and can therefore last the lifetime of an animal. This gives RFID an advantage over some tracking methods (such as GPS) as individuals never have to be recaptured to collect data. Furthermore, in contrast to direct observation, individuals can be quickly and accurately identified with minimal or no disturbance to natural behaviour.

RFID receivers can be mobile (e.g. Stuber et al. 2015), but they are often placed at attractive destinations such as feeding stations (Boisvert & Sherry, 2000; Psorakis et al., 2015) or nest-boxes (König et al., 2015) where visits are timestamped and can be recorded at high temporal resolution (<1 Hz). This technique is particularly useful for monitoring events at these destinations, for instance, co-feeding at foraging sites or entry and exit from refuges (Bonter & Bridge, 2011; Nunes-Silva et al., 2019). The precise temporal accuracy of RFID can help to measure the timing and duration of events (Milligan, Radersma, Cole, & Sheldon, 2017) and has also been successful in monitoring the affiliative movement of individuals with both spatial distribution and social interactions taken into account (Farine et al., 2014; König et al., 2015). Finally, RFID technology can be combined with other methods to remotely collect other individual-based data (e.g. vocalisations using audio recording (Hillemann, Cole, Keen, Sheldon, & Farine, 2019), cognitive testing (Croston et al., 2016) or body mass changes using recording balances (Moiron, Mathot, & Dingemanse, 2018)).

1.3.1.3 How can Eulerian methods help to identify links between movement and cognition?

By monitoring presence of individuals at specific sites of interest, behaviours most likely to be practiced at such sites can be inferred e.g. foraging at artificial feeders. The precision of the spatial locations where monitoring is conducted is helpful to in measuring the extent of space use by an animal. Furthermore, timestamped presence data can offer insights into the timings, duration and frequency of

specific behaviours, which may help to identify particular strategies that could be underpinned by cognitive processes.

1.3.1.4 Disadvantages of Eulerian methods

Logging the presence of animals only at specific locations can be problematic. Animals could be excluded from the study if they do not visit the monitored locations, limiting the sample size or collecting only partial or biased data on some individuals. Furthermore, movement paths between RFID readers or cameras must be inferred and are limited to the study area. Eulerian methods are therefore helpful when considering space use but are less suited to the study of movement paths themselves. Widely dispersing animals or those with large home ranges should be, if possible, tracked using Lagrangian methods to assess more naturalistic patterns of movement.

1.3.2 Lagrangian methods

1.3.2.1 Radio-telemetry

Radio-telemetry is one of the oldest (Lord, Bellrose, & Cochran, 1962) but still one of the cheapest methods of tracking individual wild animals. Miniaturization of very high frequency (VHF) transmitters (0.2g) (Naef-Daenzer, 2005) allows for ever smaller animals to be monitored (> 4 g) (Kays et al., 2011) and limits the impact tags can have on the behaviour of subjects. Radio-telemetry provides an option to track an animal's location at any point of the day in any terrestrial habitat (Kenward, 2001). It is an especially useful technique for cryptic or elusive species since tracking can occur from a distance. However, traditional radio tracking can be highly labour intensive, and each observer can typically only follow a single

focal individual at a time which can limit the temporal resolution of the data. Critically, in order to obtain an accurate location of a tracked animal, it must either be directly sighted after the researcher has been able to locate it with the help of radio-telemetry, in which case the observer themselves may disturb the animal and so influence its behaviour, or its location must be calculated using triangulation of directed signals from monitoring sites of known positions. This is highly labour and time intensive if done manually, requiring at least three observers to synchronise their tracking of a single individual and collect simultaneous directional data on signal strengths.

1.3.2.2 Satellite systems

Satellite systems provide an alternative to radio-tracking and collect data remotely. For ARGOS, receivers are placed in earth-orbiting satellites and can multilaterate the position of individuals on a global scale. Both satellite and terrestrial receivers calculate locations by using the Doppler effect on transmission frequency. This system has been particularly useful for pelagic species (e.g. Loggerhead turtles, *Caretta caretta* Hays et al. 1991; whale sharks *Rhincodon typus* Gifford et al. 2007) since the ARGOS system can collate and distribute data without having to relocate the individual and tag. However, the location error of the system can be several kilometres (Nicholls, Robertson, & Murray, 2007).

An alternative system, GPS, provides high spatio-temporal resolution data, enabling accurate path determination (> 5 m accuracy). For GPS systems, the GPS unit receives transmissions from satellites and collects, processes and

stores the localisations on-board. This requires larger batteries and therefore GPS units tend to be relatively large (> 5g), precluding their use on smaller species (Cagnacci, Boitani, Powell, & Boyce, 2010). GPS systems can also frequently require the recollection of the tag to retrieve data, making them unsuitable for animals that are not site faithful, although some tags allow for the remote download of the data (e.g. Fischer et al., 2018). While cheaper (~£40) GPS tags exist, there is a clear trade-off between size, features (e.g. remote downloadable) and cost that could be prohibitive for studies with large numbers of individuals, whereby state-of-the art tags can cost > £1000.

1.3.2.3 ATLAS

A novel alternative tracking method is the reverse-GPS tracking system, ATLAS (Advanced Tracking and Localisation of Animals in real-life Systems) high throughput tracking system (Weiser et al., 2016). The first system became live in Spring 2014 and uses the Time Of Arrival principal whereby tags emit a radio signal that is picked up and decoded by static receiver stations. The receiver stations then send the information to a central server where the location is estimated through multilateration and stored in a MySQL database. This means that data is collected in real-time and tags do not need to be recollected. Tags are programmable by researchers allowing for customisation of transmission rates from 1 Hz to either save battery life or increase temporal resolution. They are lightweight (<2 g) and low cost (<$20) (Toledo et al., 2014) so even studies with limited funding could tag high numbers of individuals. The system has so far been tested in the Hula Valley in Northern Isreal on Egyptian fruit bats, *Rousettus aegyptiacus;* (Toledo, Orchan, Shohami, Charter, & Nathan, 2018) and barn owls, *Tyto alba* (Weiser et al., 2016) and has been suggested to have a precision

comparable to GPS (~5 m). However, the accuracy in different habitats has not yet been tested. Tags can also be monitored through a desktop application, '*Kamadata',* which allows users to see the last known location of all tags. The implications of the software mean that users can see whether animals are leaving the study area or if movement ceases, after which researchers can quickly attempt to find the tag which may have fallen off or where the animal is deceased.

1.3.3 Concluding comments

Multiple systems are available to study animal movement, but some are more suitable for certain systems or questions than others. RFID utilises an animal's attraction to certain points and allows researchers to monitor presence, duration at that location and timing of visits. This is particularly useful to monitor activity at feeders and can therefore be utilised to effectively measure foraging behaviour. However, this approach is limited and switching to a Lagrangian approach will aid in studying more fine scale movement patterns away from affiliative locations. Radio-tracking is economically cheap but generates sparse data whereas GPS is expensive but generates data with high temporal and spatial resolution. ATLAS provides a regional-scale option that is both inexpensive and offers high temporal and spatial resolution. However, the novelty of the system means that further testing should be carried out to understand the accuracy of the system in different landscape structures.

1.4 Contexts and scales at which cognition may mediate spatial ecology

Cognition is presumed to be a key factor underlying the proximal mechanisms of movement paths (Nathan et al., 2008), yet only 1.6 % of movement ecology publications (pre-2019) pertain to the link between cognitive processes and movement decisions (Joo et al., 2019). Individuals vary in several different facets of their spatial ecology (e.g. site fidelity (Patrick & Weimerskirch, 2017), habitat selection (Leclerc et al., 2016), route choice (Campioni, Delgado, & Penteriani, 2016; Guilford & Biro, 2014; Votier, Grecian, Patrick, & Newton, 2011)). One potential explanation for individual variation in observed behaviour is that the cognitive abilities of individuals differ (Thornton & Lukas, 2012). In order to investigate the relationship between spatial cognitive ability and spatial ecology, potential pathways in which cognition may influence movement should be identified.

1.4.1 Home range behaviour

Darwin (1876) remarked that many animals choose to restrict their own space use, despite being physically capable of moving outside of this range. These confined, temporally stable areas are commonly referred to as an animal's home range (Burt, 1943; Ofstad, Herfindal, Solberg, & Sæther, 2016; Peery, 2000). These home ranges can be heavily influenced by a number of factors such the establishment of habitual routes (Presotto, Fayrer-Hosken, Curry, & Madden, 2019) or as a consequence of landscape structure e.g. habitat structure (Mitchell & Powell, 2007; Saïd & Servanty, 2005) , habitat configuration (Forman, Galli, & Leck, 1976) or resource density (South, 1999). In one of the simplest cases,

home ranges have been suggested to occur as a consequence of attraction towards focal points causing biased movement patterns (Börger, Dalziel, & Fryxell, 2008). For example, olfactory orientation towards scent marked locations (Benhamou, 1989).

Another important factor in the establishment and retention of a home range is memory (Benhamou, 1994; Van Moorter et al., 2009). Since few environments are homogenous, it frequently pays for an individual to remember both the location of resource patches or risky locations, and the most recent quality or availability of resources or level of threat at a location, to allow them to reduce uncertainty of energy intake or trade off risk of foraging against rewards (Merkle, Fortin, & Morales, 2014). Establishing a home range affords animals the opportunity to monitor the resources and risks within a particular area that constant nomadic movements into unknown environments would not allow (Börger et al., 2008; Spencer, 2012). Returning to previously visited, 'known' areas is a strong driver of animal movement and some animals will return to these areas even when other locations have been assessed (Merkle et al., 2014; Wolf, Frair, Merrill, & Turchin, 2009), perhaps to keep memories of resources up-to-date (Powell & Mitchell, 2012). Clear differences in home range size both between (Perdue, Snyder, Zhihe, Marr, & Maple, 2011) and within species (Gaulin & Fitzgerald, 1986) has been linked to differences in spatial cognitive abilities measured using behavioural assays. Furthermore, hippocampal size has been shown to differ in accordance with sex differences in home range size (Sherry et al., 1992).

1.4.2 Habitat use

Individuals differ in their use of habitats (Leclerc et al., 2016). Previous research suggests that differences in spatial cognitive ability may arise because of differential experience or use of particular habitat types. For example, populations (within and between species) differ in their particular orientation strategies (egocentric or allocentric) and these difference can be explained by the stability of landmarks within their natural habitat such that guppies, *Poecile reticulata,* from fast-flowing river populations rely less on allocentric cues than their pond dwelling counterparts (Odling-Smee & Braithwaite, 2003). Similarly, gobies (*Favonigobius lentiginosus* and *Istigobius hoesei*) from homogenous sandy shores rely more heavily on egocentric cues than gobies (*Bathygobius cocosensis* and *B. kreffti*) from spatially complex rockpools (White & Brown, 2015).

Performance in spatial tasks may also be influenced by the predictability of environments. For instance, woodpecker finches *Cactospiza pallida* from unpredictable habitat are more flexible learners than birds from more stable habitats (Tebbich & Teschke, 2014). Similarly, both hippocampal volume and neuronal numbers increase in black capped chickadees, *Poecile atricapillus* on a gradient of environmental harshness, where reliance on food caching increases over five levels of ambient temperature, day length and snow cover (Roth & Pravosudov, 2009). However, these studies have largely focussed on how an individual's spatial ability is determined by the environment in which the individual or its close ancestors lived, rather than considering whether an individual chooses to occupy particular habitats because of their inherent spatial abilities or movement strategies.

1.4.3 Navigation

Spatial memory can also influence the fine-scale movement paths through the landscape. Directed movements to previously visited areas outside the field of an animal's perceptive range are likely memory-driven (Fagan et al., 2013). Remembering locations, such as profitable foraging patches, and the relative position of each of these, can lead to a refinement of transitory paths towards the desired location as experience increases. Specifically, increases in efficiency can be achieved by reducing turning frequency to travel straighter routes (Wilson et al., 2013) and multiple studies have found that straightness of paths increases with experience. For instance, grey seal pups, *Halichoerus grypus*, develop the characteristics of their transitory movements to be faster and straighter as they age (Carter et al., 2019). Similarly, bumble bees, produce faster and straighter routes between the hive and a feeder as their experience increases across a number of trials (Osborne et al., 2013).

Many central place foragers will develop and optimise routes that allow visitation to sequential foraging sites (traplining) (Lemke, 1984; Tello-Ramos, Hurly, & Healy, 2015). Repeatable routes allows for individuals to outcompete other foragers (Ohashi, Leslie, & Thomson, 2008) by using shorter or less energetically costly routes (Ohashi, Thomson, & D'Souza, 2007; Saleh & Chittka, 2007). In bumblebees, *Bombus terrestris*, stable and optimal traplines are established after over multiple foraging bouts, reducing the distance travelled by 80% (Lihoreau et al., 2012). In honeybees, *Apis mellifera*, more efficient routes are established at larger spatial scales (Buatois & Lihoreau, 2016), presumably because investment in route learning increases with energetic cost of suboptimal routes.

Memory is likely to be a key component in complex, heterogenous landscapes and may aid in extreme route fidelity to long range migratory movements (Jakopak, LaSharr, Dwinnell, Fralick, & Monteith, 2019; Merkle et al., 2014, 2019; Sawyer, Merkle, Middleton, Dwinnell, & Monteith, 2019). Models of ungulate migrations were two to four times closer to their end destination when memory was included in the model, indicating more direct routes were taken (Bracis & Mueller, 2017). Wide ranging species such as African elephants, *Loxodonta Africana*, can change their trajectories to move directly towards watering holes from up to 50 km away (Polansky et al., 2015). Similarly, knowledge of the temporal fluctuations of resource waves shapes the long-range migrations of blue whales, *Balaenoptera musculus* (Abrahms et al., 2019).

1.4.4 Concluding comments

Cognition is likely to play an important role in multiple areas of animal movement ecology, from broad scale range use and habitat preferences to fine scale movement decisions. Each of these examples of movement ecology is inevitably inter-linked, i.e. movement paths take place in habitats which can constitute the home range of an animal. We therefore may expect that performance on the same or similar cognitive tasks will yield insight into the cognitive mechanisms underlying spatial decision making at various scales and contexts.

1.5 The scope of this thesis

While there have been numerous attempts to provide theoretical models of the interactions between spatial cognition and movement ecology (Benhamou et al.,

1990; Bracis et al., 2015; Bracis & Mueller, 2017; Fagan et al., 2013; Spencer, 2012; Van Moorter et al., 2009), empirical studies are sparse. In this thesis, I aim to identify whether there is a mechanistic link between spatial cognitive ability and movement ecology. I predict that this link could exist in the following ways.

An animal's home range is suspected to be the area within which an animal can remember resources. While it seems to be the case that broad-scale measurements of home range size correlate with spatial ability (Gaulin & Fitzgerald, 1989; Perdue et al., 2011), little is known about the actual use of foraging sites within a home range, yet it is these sites that could be a key determinant of movement behaviour, and consequentially the size of a home range. Specifically, if home ranges are the total area in which an animal is able to keep updated in memory (Powell & Mitchell, 2012), and important sites encoded in memory are likely to be (perhaps mostly) foraging sites (the profitability of which should be kept updated), then I would expect individuals with better spatial cognitive ability to utilise a more diverse range of foraging sites (**Chapter 2**).

Movement between places of interest, such as foraging sites or refuges could be quicker and less tortuous for individuals with better spatial cognitive ability. This may result in arriving at foraging sites earlier than others if all individuals aim to forage at similar times, perhaps in the morning (**Chapter 3**). Furthermore, in a novel environment we may expect individuals with better spatial cognitive ability to learn about spatial information more quickly and therefore develop more efficient routes at a faster rate, which we expect would be straighter and/or more

quickly travelled (Carter et al., 2019; Osborne et al., 2013) (**Chapter 5**). Efficiency is a particularly difficult trait of movement trajectories to isolate in free-roaming populations because we can only attempt to infer the goal location of an animal from its end location; since individuals will start from different places and may visit different foraging sites this is not a trivial task. Recently developed analytical tools, such as hidden Markov models (Carter et al., 2019; Michelot, Langrock, & Patterson, 2016) may provide a starting point to understand the movement decisions of free-roaming animals by allowing a "bottom-up" approach to analysis beginning with path segments (Ironside et al., 2017), specifically transitory movements. Finally, individual differences in preference for spatial cue types may not be a result of experience in a particular habitat but may instead be an inherent preference. If this is the case, then I would expect that individuals with different preferences for particular cue types may differ in their habitat use (**Chapter 6**).

1.6 Requirements of a study system

To effectively study the influence of cognitive traits on movement and space use, a study system must meet several criteria. First, robust measures of cognition should be relatively simple to obtain on large numbers of individuals to maximise statistical power and mitigate for any issues that may arise that can be attributed to, for example, differential or biased participation in cognitive tasks or survival of individuals in the wild. Ideally, performance scores should be obtained early in life, when individuals have developed in an environment where it is possible to control for experience. To achieve this, animals should be reared in identical conditions and subject to cognitive tasks following habituation and shaping procedures to maximise participation and reduce stress. Second, accurate

measures of movement, and/or space use are required to measure natural behaviours in a real-world environment. To achieve this, a free-living species that is large enough to follow using Lagrangian tracking methods should be used. This constitutes a particular challenge as to an ideal study species, because captive-reared individuals (ideal for obtaining accurate cognition measures) are seldom released into the wild (necessary for obtaining natural movement and space use data). One resolution is to use a study species that has an established reintroduction protocol, in which they spend their early lives being reared under controlled conditions but are later released into the wild. Furthermore, individuals should all be introduced to the same environment at the same time where they can experience the same landscape structure, reward and risk opportunities and social pressures and where changes in movement patterns or space use over time can be recorded simultaneously.

1.7 The Pheasant

The pheasant provides a unique and unusual opportunity to study the relationship between cognition and movement ecology. Pheasants eggs can be artificially incubated and large numbers can be hatched on the same day. Chicks are precocial can be reared successfully in captivity without parents before being tested on a range of cognitive tasks, often adapted from work on chickens (Nicols, 2015) from ~3 weeks old (Madden, Langley, Whiteside, Beardsworth, & van Horik, 2018; van Horik, Langley, Whiteside, Beardsworth, & Madden, 2018; van Horik, Langley, Whiteside, & Madden, 2016, 2018). This means that captive reared individuals can be tested at the same age, while controlling for experience and reducing maternal effects.

Pheasants have a long history of being released in the UK for hunting, and management of birds post-release has been well documented (Hill & Robertson, 1988). At the age of 6-10 weeks old pheasants are subject to a soft release where they are placed into a woodland enclosure that is surrounded by fencing and provides access to water and food, allowing birds to acclimatise to living in the 'wild'. This semi natural environment is free from terrestrial predators but due to an open roof, which allows the birds to disperse, it is not free from aerial predators. Pheasants then slowly disperse into the wider, environment over the following month or two. Crucially, this soft release provides an excellent opportunity to monitor behaviour *de novo*, since all birds are released into the same novel environment simultaneously.

In the wider landscape, supplementary feeding sites are frequently provided for released pheasants in the form of barrel feeders filled with grains. This provides an opportunity to monitor foraging behaviour using either camera traps or RFID readers, since released pheasants use these sites as their primary food source (Draycott, Woodburn, Carroll, & Sage, 2005; Whiteside, Sage, & Madden, 2015). In addition, pheasants are relatively large birds (1-2 kg) which allows them to carry telemetry tags weighing up to ~ 50 g, although much smaller tags should be sourced when possible (Kenward, 2001). Once pheasants disperse from their enclosure, they tend to use habitats within ~30 m of woodland edge (Hill & Robertson, 1988; Robertson, 1997). Pheasants (especially captive reared pheasants Bagliacca, Falcini, Porrini, Zalli, & Fronte, 2008) do not disperse very far, generally less than 2-3 km from their release site (Wilson, Drobney, & Hallett, 1992), making them excellent candidate subjects for use with regional tracking systems such as ATLAS. The availability of PIT tags and ATLAS as tracking

systems allows the monitoring of hundreds of free-roaming individuals. Furthermore, their limited range allows for detailed field searches and the involvement of local citizens to monitor their fates and attain an unequivocal measure of survival in relation to both cognitive and physiological traits that can be collected pre-release (Whiteside, Bess, et al., 2018).

1.8 Specific questions within this thesis

In this thesis, I address four specific questions (identified in **Section 1.5**) to attempt to empirically identify links between spatial cognition and movement ecology using the pheasant as a model system. I took a controlled, experimental approach and all pheasants were reared under standardised conditions and tested on one or more spatial cognitive tasks before being released, although these differed slightly depending on the cohort.

In 2016 I measured spatial cognitive ability using three tasks, all aimed at measuring the spatial domain: two 1 x 2 small scale foraging grid tasks in opposite orientations (binary choice) which I assessed with a general performance score and one Barnes maze style task which was assessed using accuracy criteria. I monitored pheasants with PIT tagged leg rings at foraging sites using RFID antenna situated under artificial feeders. I assessed the diversity of foraging site use within the restricted range of the release enclosure to control for habitat structure and predicted that birds with better spatial cognitive ability would utilise a more diverse range of feeders (**Chapter 2**).

Using the same population as in **Chapter 2**, I assessed temporal aspects of foraging behaviour at all feeders across our field site. I tested whether spatial cognitive ability influenced the arrival times of pheasants at their first foraging bout of the day (**Chapter 3**). I predicted that birds with better spatial cognitive ability would arrive at feeders sooner than others as a consequence of being able to remember quicker routes, or perhaps leaving a refuge sooner because they remembered safer routes.

In **Chapter 4** I assess the accuracy, precision and reliability of a novel reverse-GPS tracking system (ATLAS) that provides high spatio-temporal data at relatively low cost compared to satellite tracking units. This system has not been formally tested in landscapes like our field site, which is a hilly, heterogenous habitat. I therefore assessed this system for use in subsequent experiments.

In **Chapter 5**. I test the assumption that better spatial ability (measured in a Barnes maze style task) results in more efficient paths between sites of interest such as foraging patches or refuges (transitory paths) using the ATLAS system to track individuals. I predicted that birds with better (in this case, more accurate) spatial cognitive ability would develop their transitory paths more quickly than poor performing individuals.

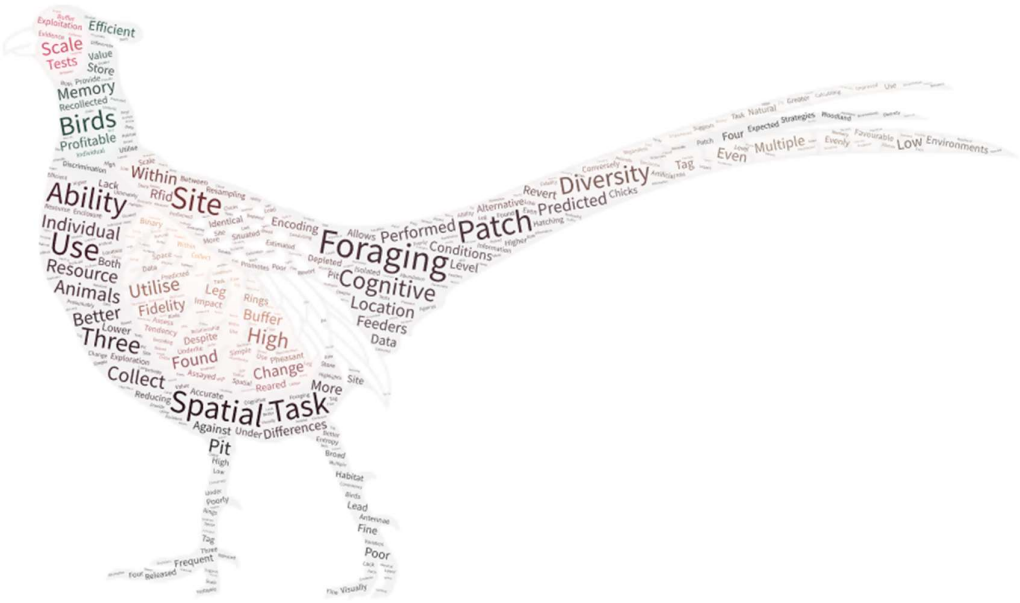
Finally, in **Chapter 6**, I assessed which orientation strategy individuals use on a complex maze task (using a dual strategy maze task and a single-strategy probe trial) and tested whether this predicted differential use of habitats after release.

This allowed me to test explicitly whether spatial abilities were the cause or consequence of space use in the wild.

1.9 Conclusion

This thesis is one of the first, if not the first attempt at understanding how individual differences in spatial ability impact the foraging and movement decisions of free-ranging animals. I combine measures of spatial ability with multiple assessments of spatial ecology to identify the consequences of spatial ability on the spatial (**Chapter 2**) and temporal (**Chapter 3**) aspects of foraging behaviour and assess both fine-scale (movement trajectories: **Chapter 5**) and broad-scale (habitat selection: **Chapter 6**) movement behaviour.

2 Individual differences in spatial cognitive ability predicts the use of multiple foraging sites in an enclosed but natural habitat



2.1 Abstract

Encoding profitable locations to memory can aid animals in the efficient exploitation of resources. Memory can act as a buffer against changing environments by reducing the need to revert to exploration if resources in one location are depleted. Frequent resampling of alternative sites, even when conditions are favourable, allows for more accurate memories to be recollected if conditions were to change. The tendency of animals to use multiple foraging sites, despite predictable environments, seems to vary at an individual level and differences in the ability to collect, store or utilise spatial information (spatial cognitive ability) may impact these strategies. We predicted that individuals with better spatial cognitive ability would have lower site fidelity and utilise multiple foraging sites evenly (high foraging patch diversity). Conversely, we expected individuals with poor spatial cognitive ability to have high site fidelity (low foraging patch diversity). We assayed the spatial cognitive ability of pheasant chicks, reared in identical conditions from hatching, on a battery of three spatial cognition tests. We released these birds into an enclosure within their natural habitat (woodland) and collected foraging data using PIT tag leg rings and RFID antennae situated under four visually isolated artificial feeders, which were predictable in both location and resource value. We estimated the diversity of foraging patch use by calculating the entropy of use of these feeders. We found that one of three spatial tasks predicted foraging patch diversity; birds that performed better on a simple binary discrimination task had higher foraging patch diversity than birds that performed poorly. This suggests that improved spatial cognitive ability promotes the use of a greater diversity of foraging patches, regardless of the predictability and abundance of resources. However, we found no relationship between performances on the three presumably spatial cognition

tasks. The lack of consistency within individuals highlights the importance of conducting a battery of tasks to assess individual differences in cognition. Nevertheless, we provide evidence that variation in cognitive abilities underlie the fine-scale foraging decisions that can ultimately lead to broad-scale space use.

2.2 Introduction

The cognitive underpinnings of spatial ecology have had little empirical attention considering the presumed importance of memory in determining movement decisions (Nathan et al., 2008). Encoding profitable locations to memory is thought to increase the efficiency of resource exploitation (Van Moorter et al., 2009) and reduce the need for potentially costly exploration (Eliassen, Jørgensen, Mangel, & Giske, 2007). Furthermore, remembering multiple patches can buffer against changing environments, such as depleting resources (Kembro, Lihoreau, Garriga, Raposo, & Bartumeus, 2019) but keeping information about resource profitability up to date may require frequent revisits to known resources. Many species consistently revisit specific locations, such as breeding sites, refuges and foraging patches (Bradshaw, Hindell, Sumner, & Michael, 2004; Piper, 2011) and will restrict their total space use to encompass these important locations within their home range. Within species, individuals differ in their foraging strategies, specifically their fidelity to foraging sites (e.g. black-legged kittiwakes *Rissa tridactyla* (Harris et al., 2020), black-browed albatrosses *Thalassarche melanophris* (Patrick & Weimerskirch, 2017), herring gulls *Larus argentatus* (Van Donk, Shamoun-Baranes, Bouten, Van Der Meer, & Camphuysen, 2019)), even in highly predictable environments. The size of a home range, which comprises important areas that an animal visits, has been suggested to be the maximum area within which memory of spatial information can be kept up to date (Powell & Mitchell, 2012; Tolman, 1948). If memory is key to the exploitation of resources, then inter-individual differences in the ability to collect, store and utilise spatial information i.e. spatial cognitive ability, could play an important role in mediating the number of patches that are regularly visited, thus influencing foraging strategy and space use.

Cognitive abilities have been suggested to have a heritable basis (Croston, Branch, Kozlovsky, Dukas, & Pravosudov, 2015; Sauce et al., 2018; Smith et al., 2005) on which selection can act (Thornton & Lukas, 2012). Variation in spatial cognitive ability in particular has been linked to several fitness proxies (e.g. survival (Maille & Schradin, 2016b; Sonnenberg et al., 2019); reproductive investment (Branch et al., 2019; Shaw et al., 2019) and mating success (Shohet & Watt, 2009; Smith et al., 2005)), but the direct relationship between spatial cognitive ability and spatial ecology has only been tested at relatively broad scales. For instance, males have better spatial cognitive ability than females in some polygynous species, where males have larger home ranges (Gaulin & Fitzgerald, 1986; Perdue et al., 2011). Identifying individual differences in space use is not a trivial task. Habitat heterogeneity (Switzer, 1993) can have strong influences on an animal's use of space and is difficult to control for in free-roaming animals. However, even in an enclosed environment, spatial cognitive ability influences the amount of space an individual uses (e.g. in the domestic chicken, G*allus gallus domesticus* Bessa Ferreira et al., 2019). The proximal mechanisms underlying these movement decisions are still unclear, but individually limited memory of locations, such as profitable foraging patches, could drive these broad-scale differences.

Foraging decisions are an essential factor influencing animal movement (Nathan et al., 2008) in which animals try to reduce costs while maximising the benefits of their choices (Charnov, 1976). For species that utilise patchy resources, it is beneficial to learn and remember the location of profitable patches (Bracis et al., 2015). The knowledge of the location of multiple patches provides a buffer against changing values of the patches or uncertainty about their value (Bartumeus et al.,

2016; Kembro et al., 2019). For example, an individual that returns to a patch that has become unprofitable, perhaps because it is depleted or increased in predation risk, can opt to move to an alternative patch without having to revert to exploring the environment for an unknown patch. For this strategy to be viable, frequent resampling may be required to keep up to date information on the profitability of alternative patches in memory. This would likely lead to lower site fidelity for one location and a more even usage of multiple foraging sites (high foraging patch diversity). Alternatively, if spatial cognitive ability is poor, an individual may have high site fidelity and rarely explore other options (low foraging patch diversity).

To investigate whether foraging patch diversity is linked to spatial cognitive ability, a study must meet several criteria. First, an accurate measure of spatial cognitive ability should be obtained. To assay spatial cognitive ability, inferences must be made from performances on behavioural tasks that require animals to learn to use spatial information, typically to retrieve a reward. These tasks often imitate foraging scenarios whereby food items are consistently hidden in the same location within an array of potential locations, usually arranged in a grid (Saleh & Chittka, 2007; Sulikowski & Burke, 2010; Sutherland & Gass, 1995), open ring or square arrays (Croston et al., 2016; Perdue et al., 2011) or radial-mazes (Olton & Samuelson, 1976). Different tasks may probe alternate facets of cognitive ability, but we might expect that an individual's performance in a suite of tests each intended to assay similar cognitive abilities (for example spatial cognitive ability or associative learning) would be consistent (Völter et al., 2018). Consistency in task performance within the same individual is rarely addressed (Völter et al., 2018) but we cannot conclude that a 'general' spatial cognitive

ability explains variation in patch use unless we specifically test whether an individual's performance is consistent across putatively related tasks and whether their patch use relates to performance in each task. We may expect spatial tasks of different scales to be unrelated and represent specific abilities within tightly foccussed domains rather than a more general spatial ability as has been shown in some studies (Guigueno et al., 2015; Sauce et al., 2018). Second, these tests should be conducted on known individuals while controlling for factors that may influence performance or participation, such as age (Drapeau et al., 2003), sex (Astié et al., 1998; Galea et al., 1996; Lucon-Xiccato & Bisazza, 2017), prior experience on tasks (Harlow, 1949) or their ontogenetic environment (Whiteside, Sage, et al., 2016). Although spatial cognitive ability can be assayed in wild animals (Ashton et al., 2018; Branch et al., 2019; Shaw et al., 2019), controlling for these effects can be difficult, therefore a study species that can be raised in captivity in large numbers is desirable. Third, it is necessary to monitor numerous foraging events by individuals at multiple locations. Critically, it is desirable to compare the use of resources of similar value, located in the same landscape because this permits control for heterogeneity of habitat which can, of itself, affect foraging choices (Roese, Risenhoover, & Folse, 1991). This would allow an assessment of the use of sites of equal value and accessibility which helps in making a reliable comparison of the diversity of patches used.

The pheasant, *Phasianus colchicus*, offers a useful system with which to assess the links between spatial cognitive ability and patch use. First, pheasants can be reared from hatching in large numbers while accounting for experience and age and have been successfully assayed on a number of spatial tasks (e.g. radial arm mazes (Whiteside, Sage, et al., 2016), binary spatial discrimination tasks

(Langley, van Horik, Whiteside, & Madden, 2018b, 2018a), foraging grids (van Horik, Langley, Whiteside, Laker, & Madden, 2018)). Second, in the UK, pheasants are routinely released into the wild to supplement hunting stock. 'Soft-releases', whereby 6-10 week-old birds are released into large, open-topped outdoor enclosures (hereafter 'release pen') are a frequent method used by gamekeepers. Release pens are frequently situated in woodland and therefore contain natural habitat, as well as predictable feeding stations (refilled regularly) while they acclimatise to the wild. These areas provide an excellent opportunity to measure foraging patch use in a semi-natural environment while controlling for habitat heterogeneity. Although the natural movement and space use of pheasants differs with age, sex (Whiteside et al., 2019) and mass (Snyder, 1985), these effects can be accounted for since pheasants can be sexed visually and birds that have been artificially reared and released are all of known ages.

We assessed spatial cognitive ability in pheasant chicks, aged between 3 and 6 weeks old, by presenting them with two spatial tasks of different spatial resolutions (a binary choice tasks with ~1 cm difference in location and a 2 x 2 foraging grid with ~50 cm differences) to identify whether our tasks both assessed the same cognitive processes. If there is a 'general' spatial cognitive ability, then we expected the tasks to correlate strongly with one another. However, evidence suggests that differences in spatial scale may invoke differential cognitive processes, although these may not be completely disassociated (Hegarty, Montello, Richardson, Ishikawa, & Lovelace, 2006). There are very few studies that have assessed within-individual performances between small- and large scale spatial tasks (although see Guigueno, Macdougall-Shackleton, & Sherry, 2015; Sauce et al., 2018). Yet if there is a difference in spatial cognitive ability

between scales, we do not know, *a priori,* which scale would influence real world space use. In this case, it is important to assess the impact of the different facets of spatial cognitive ability on foraging strategies. We released the birds at 10 weeks old into the same large release pen in woodland and measured their use of four artificial feeders positioned in visually isolated areas of the pen. We modelled the effects of spatial cognitive ability, motivational traits (measured at the same time as cognition), sex and mass on the diversity of feeder use. We predicted that individuals that exhibited good spatial cognitive ability would utilise a higher diversity of feeders. We expect this may occur despite an abundance of food at all foraging sites as those with better spatial memory may be able to utilise a different foraging strategy, frequently resampling multiple foraging patches and buffering against change in the value of one or more patches.

2.3 Methods

2.3.1 Subjects and Housing

Two groups of 50 pheasant chicks were housed in identical (1.75 m x 2 m) heated enclosures (Figure 2.1) from one day old between 19th May and 21st July 2016 at North Wyke Rothamsted Research farm (Devon, 50º77'N, -3º9'W). Within the enclosure, but separated by a sliding door, was a testing chamber (0.75 m x 0.75 m). A mesh partition separated the main enclosure from a post-testing area which was raised when we were not testing any birds. At four weeks old, the chicks were given access to an outdoor enclosure (4 m x 12 m) which was directly connected to the heated enclosure (through the post-testing area). Birds were individually identifiable from two weeks old using numbered patagial wingtags

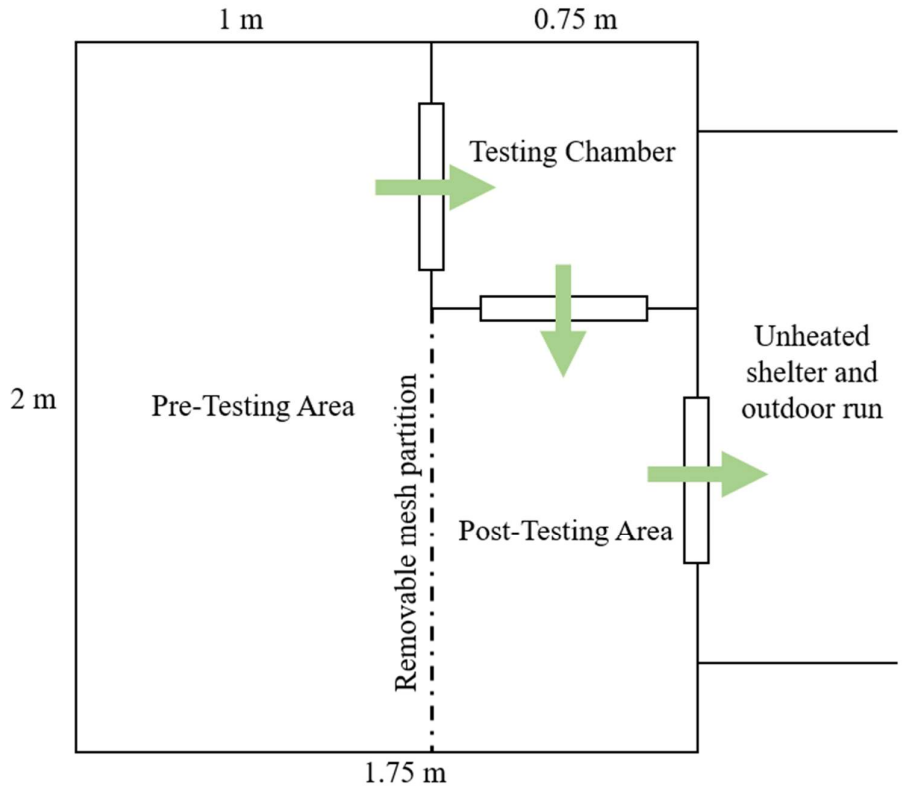


Figure 2.1 Schematic of housing and testing areas for pheasant chicks in captivity. Mesh partition could be raised after testing finished to allow birds to use the full area of the enclosure when no testing was taking place.

(Roxan Ltd, Selkirk, UK). Chicks were given *ad libitum* access to age-specific commercial chick crumb (Sportsman Game Feed) and water.

2.3.2 Training

2.3.2.1 Habituation to humans

From one day old, chicks were shaped to the cognitive testing procedures. First, the chicks were habituated to the presence of the experimenters. Every experimenter wore a standard white lab coat and a red hat during all shaping and subsequent testing sessions until the chicks were released. Experimenters tapped and scratched the chick's food bowls, allowing chicks to habituate to human hands, movement and faces while humming a three or four syllable tune (specific to each enclosure) so that chicks associated the tune, tapping and scratching sounds and the experimenter with a food reward. We did this so that these actions could later be used to attract birds to the testing chamber without inducing stress. Each habituation session was 20 minutes long and all experimenters habituated each pen at least once a day for the first 4 days of life.

2.3.2.2 Habituation to testing chamber and testing equipment

At five days old, we began to shape the chicks to voluntarily enter the testing chamber and habituate them to the test apparatus for subsequent tasks (a 45 cm x 15 cm white box with 10 wells of 2 cm diameter x 1.8 cm deep in a 5 x 2 array, referred to as a poke box). We first scattered mealworm rewards over the poke box and the floor of the testing chamber and allowed groups of five birds to enter from the aviary. After the mealworms had been consumed, birds were released into the post-testing area.

2.3.2.3 Training for the first cognitive task

Once all birds were rapidly searching for mealworms in the wells of the pokebox, we covered the wells with opaque tissue paper to hide the contents from the subjects. In the first few rounds of training we opened some of the wells slightly to encourage pecking through the paper. Pecking through the tissue paper and into any of the ten wells gave access to a mealworm reward and has proven a successful method for measuring cognitive abilities in pheasants (Langley, van Horik, Whiteside, & Madden, 2018a; van Horik, Langley, Whiteside, & Madden, 2018). We slowly reduced group sizes as the birds habituated to the environment and ceased shaping once each bird was able to enter the testing chamber alone and open each well.

At the end of the first training task (at 3 weeks old), birds were pecking through the paper on all wells and expected rewards in each well. We introduced the birds to a binary choice training task before starting the cognitive testing so that the birds had the opportunity to learn that that only one choice could be made per trial (as opposed to the previous shaping task) and that wrong choices yielded no access to the reward on that trial. This ensured that during the first spatial cognition task (a binary choice task), the birds needed only to learn the spatial location of the reward. The two wells in the training apparatus were arranged horizontally. The left well contained 3 mealworms; the right well was blocked with black card so that its reward could not be accessed. Both were covered with tissue paper, so the wells looked identical. After each choice, the wells were replaced for the next trial and birds could not make a second choice during the same trial. The training took place over five sessions per bird, with testing starting at 9 am and 2 pm on the 6th -7th June 2016 and at 9 am on the 8th June 2016.

Each training session consisted of 10 trials giving each bird the opportunity to complete 50 training trials. Ninety-five individuals completed all 50 training trials.

2.3.3 Cognitive Tasks

For all cognitive testing, individuals entered the testing chamber alone and all birds were given identical opportunities to participate in the tasks. We recorded the order in which birds entered the testing chamber (test order) and calculated an individual's median test order over 24 testing sessions (including the binary choice training task, the following 2 cognitive tasks and one other task used for a separate experiment). A single session entailed the bird entering the testing chamber once, but in the Top-Bottom binary task multiple trials could take place in one session.

2.3.3.1 Small-scale task: Top-Bottom Binary Choice

At 3.5 weeks old, we gave the birds a binary choice task. The same style of apparatus was used as in the training task but the two wells were arranged vertically (Figure 2.2a) with one well closer to the bird and the other further away. Birds were centralised using a dead mealworm lure between the two wells. The top well contained 3 mealworms and the bottom well was blocked with black card and both were covered with tissue paper. Again, birds were tested during five sessions, with testing starting at 2 pm on the 8th June 2016 and at 9 am and 2 pm on the 9th - 10th June 2016. Each session consisted of 10 trials allowing each bird the opportunity to complete 50 trials for this task. Ninety-nine individuals completed all 50 trials.

2.3.3.2 Large scale task: Cup Task

At 5 weeks old, the pheasants were presented with a task testing spatial discriminations at a larger-scale (~50 cm gap between potential locations of reward). The task used the entire area of the testing chamber with a plastic cup located in each of the four corners (Figure 2.2b). Birds were lured to the centre of the chamber by a clearly visable mealworm reward. The cup situated closest to the observer and furthest from the entrance door contained a mealworm reward not visible to the tested bird when at the centre of the enclosure. If a bird approached within 12 cm (~1 body length) of the centre of any cup (shown by a line marked on the floor) then the bird was considered to have inspected that cup. Visits were counted until the rewarded cup was chosen and the reward taken. Each session consisted of only one trial and all birds had the opportunity to complete 6 sessions taking place at 2pm on the 21st June, 9 am and 2 pm on the 22nd and 23rd June and at 9 am on the 24th June. Ninety two birds completed all 6 trials.

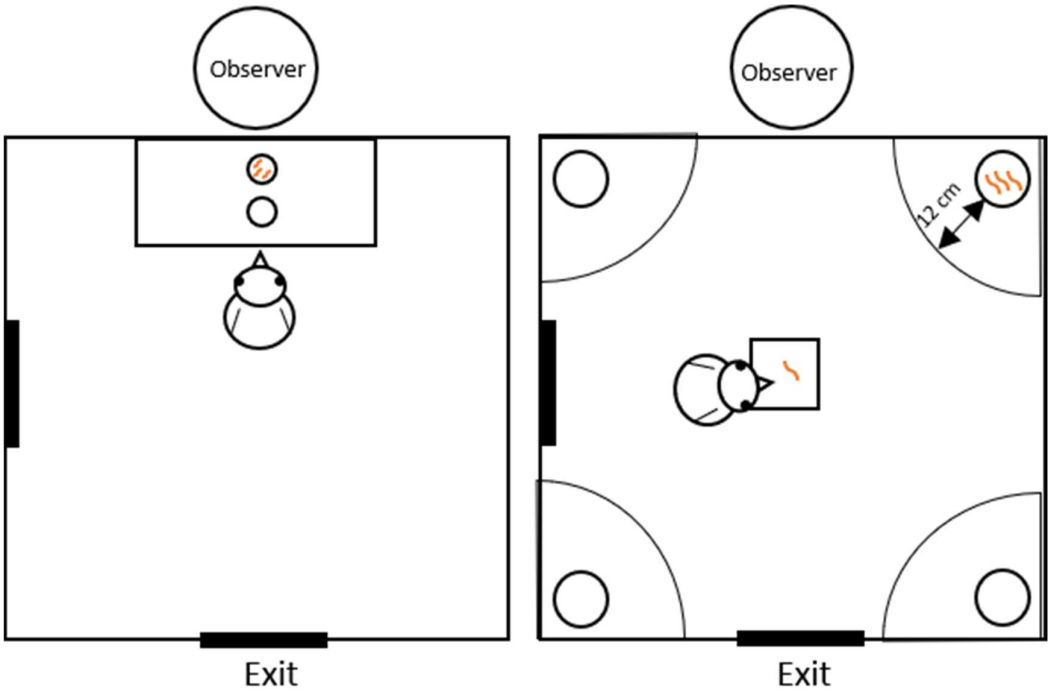


Figure 2.2 Schematic of testing chamber for each task. a) Top-Bottom binary choice task c) Cup Task

2.3.4 Release

At 10 weeks old on the 21st July 2016, the pheasants were weighed (Slater Super Samson spring balance – precision 5 g), sexed (by plumage) and had Passive Integrated Transponder (PIT) tag rings attached to their legs. They were then released into an open-top pen (~ 4000 m^2) located in a wooded area of North Wyke Farm within which the birds could roost and shelter. It was surrounded by 2 m high fences and an electric fence to deter terrestrial predators. Water was provided *ad libitum*. Additionally, four barrel-feeders, containing a mix of chick pellets (Sportsman Game Feed) and wheat, were positioned in clearings within the pen to permit *ad libitum* feeding (Figure 2.3). Released pheasants are highly reliant on artificial feeding stations (Draycott, Hoodless, Ludiman, & Robertson, 1998; Whiteside et al., 2015) and we therefore expect that the feeders are a preferred foraging site for the birds. Feeders could be accessed from multiple

directions, reducing competition between individuals. A Radio-Frequency Identification (RFID) reader (Spec: custom flat aerial with plastic (35 cm diameter) coating (IB Technology), covered with artificial grass) was placed under each barrel feeder to log visits from each bird. Although birds were able to disperse into the surrounding environment, this was discouraged by experimenters circling the pen at dawn and dusk to guide birds back into the pen via one-way funnels for the first month after release. The surrounding farm consists of a mix of grassland and woodland. There was no game shooting or predator control on the farm.

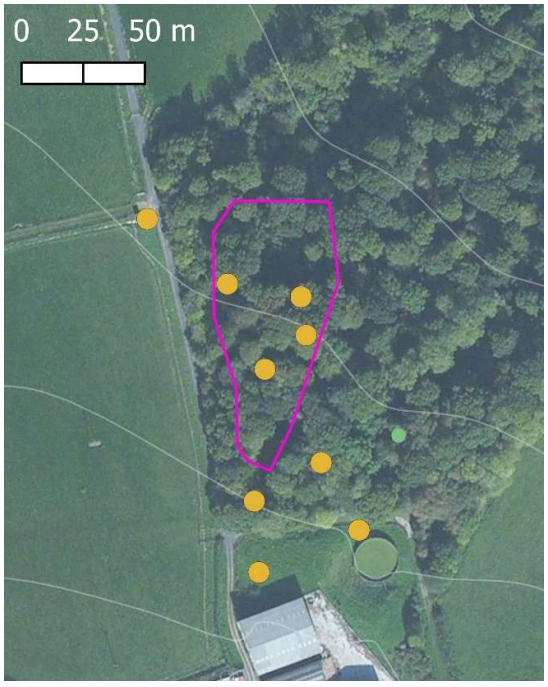


Figure 2.3 Layout and location of release pen (pink outline) with feeders (yellow circles) located both inside and outside of the pen.

2.3.5 Measuring Feeder Diversity

The RFID readers scanned for PIT tags once per second. In some cases, individuals might step off the antennae briefly but continue foraging for dropped wheat next to the feeder before standing on the antennae again to use the feeder.

To ensure we counted these foraging instances as a single visit to a feeder, we defined separate visits as having an inter-detection interval of > 15 mins. Feeders were located in separate clearings within the woodland, visually isolated from one another by dense vegetation, placed 15 - 40 m apart (Figure 2.3).

From 10 days post-release the birds began to disperse out of the release pen (Figure 2.4), therefore we limited the analysis to birds that only visited feeders within the release pen during the first 10 days after release and which had been detected at feeders at least 8 times. We never detected these birds outside the release pen during this time so we have assumed that these birds had not left the release pen and therefore the maximum number of feeders they could have visited were the four within the pen. This standardises the opportunities for feeder use across all included birds.

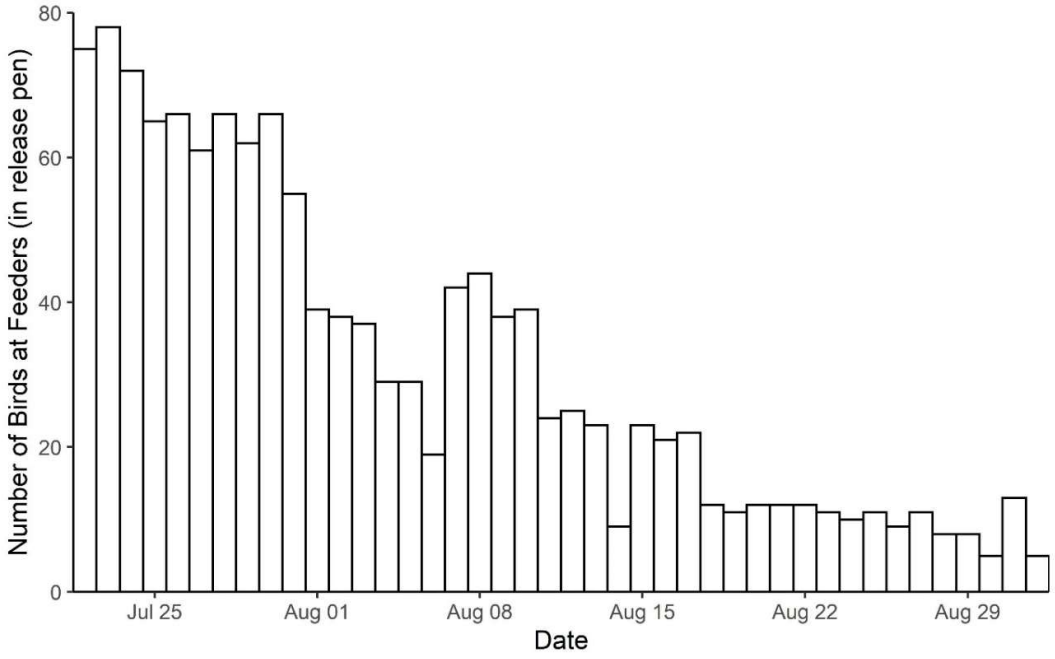


Figure 2.4 Cut-off date was selected (1st August) based on the number of detections of unique birds at feeders in the release pen. Due to dispersal this declined rapidly.

2.3.6 Analyses

All analyses were performed in R (v3.4.3) (R Core Team, 2019) using the R studio wrapper (v1.1.423) (RStudio Team, 2018). Forty-one birds (23 females, 18 males) completed all training trials, both cognitive tasks, stayed within the release pen for the first 10 days and were detected at feeders at least 8 times within this period.

2.3.6.1 Did the birds learn the cognition tasks?

We assessed whether, at a population level, the pheasants showed improvement in each of the cognition tasks, indicative of learning. We fitted generalized linear mixed models (GLMM) from the *lme4* (v1.1-21) R package (Bates, Maechler, Bolker, & Walker, 2015). For the Top-Bottom task, we used a GLMM with a binomial error structure and a logit link function with choice on each trial included as the response variable (0 = incorrect, 1 = correct). We included trial number, sex, test order and body mass as fixed factors within the model. Bird ID was included as a random effect. All continuous variables were scaled and centred using the *scale* function from base R before fitting the model. We used stepwise model selection using the drop1 function in base R to produce a minimal model.

For the cup task, we fitted a GLMM with a Poisson error structure and a log link function with a count of the number of errors made before attaining the reward as the response variable. Again, we included trial number, sex, test order and body mass as fixed factors and Bird ID as a random effect in the model. All continuous variables were scaled and centred using the *scale* function from base R before

fitting the model. We used stepwise model selection using the drop1 function in base R to produce a minimal model.

2.3.6.2 Assessing individual-level performance on the top-bottom binary discrimination task

Following the approach of previous studies (Langley, van Horik, Whiteside, & Madden, 2018b, 2018a), we calculated scores for the binary choice task by fitting a generalized linear model with a binomial error function for each bird, with choice (1 correct, 0 incorrect) as the response variable and trial number as a fixed factor. We calculated the probability that an individual would choose correctly on their final trial (X50) using the equation (where β0 is the intercept and β1 is the slope from the model):

$$X50 = \frac{1}{1 + exp(-(\beta 0 + (\beta 1 \times 50)))}$$

If the value of X50 for a given individual was below 0.60 probability of a correct choice, we concluded that the individual had not improved sufficiently to be confidently classified as learning or having learnt the task. It is only important to know that these individuals did not learn the task and we consider that the variance within their 'non-learning' is irrelevant. To reduce the leverage that these individuals may have on subsequent analysis and eliminate the variance in 'non-learning', we assigned all non-learners a floor-value for their X50 of 0.50 i.e. choosing at chance levels. Of the ninety-nine individuals that completed all 50 trials, 16 birds were non-learners and 83 birds learnt or showed improvement in the task.

2.3.6.3 Assessing individual-level performance on the cup task

Completing a trial with no errors indicates success on a trial. However, with only four options, birds have a 0.25 probability of making a correct choice by chance on each trial but the probability of completing multiple trails with zero errors consecutively decreases with trial number. Many studies utilise a criterion approach to measuring learning and count the number of trials taken to reach criterion e.g. 7 consecutive sucesses (Wong & Judd, 1973). Due to temporal constraints (to complete other tasks before release) and because we wanted to control for experience in captivity, all birds completed 6 trials and we took a reverse-criterion approach and measured the maximum number of consecutive trials completed with no errors during the trials. Birds with higher scores had completed more trials without errors consecutively and were deemed as having better spatial cognitive ability.

To determine if the birds were learning at a population level, we calculated the distribution of scores we would expect by chance for the cup task by simulating scores for 41 individuals over 6 trials where all individuals had a probability of 0.25 to complete a zero-error trial. We repeated this 10,000 times and calculated the mean score of simulated birds with confidence intervals (using the t-distribution) and compared this to the real data. We also calculated the expected number of individuals obtaining each possible score (0-6) with confidence intervals and compared these to the frequencies of scores we obtained.

2.3.6.4 Were performances between tasks correlated?

We used a corrected spearman's rank correlation to assess whether there was a relationship between performance in a small-scale spatial task and a larger scale spatial task in pheasants.

2.3.6.5 Assessing feeder use

We assessed the diversity of feeder use by calculating Shannon's entropy for each individual considering their patterns of visits across all four feeders in the release pen. We investigated the effects of spatial cognitive ability on entropy by fitting a gaussian general linear model with an identity link function. We fitted cognitive performance (X50 for the Top-Bottom task; maximum consecutive trials with no errors for the Cup task), non-cognitive factors (mass at release (hereafter mass), sex, test order) and total number of visits to feeders (to account for variation in detections of each bird, since the total number of visits to feeders varied among the birds (range = 9-78, mean ± SD = 31.32 ± 16.01) as factors in the full model. We used stepwise model selection using the drop1 function in base R to produce a minimal model. Number of visits to feeders was retained in the model as a fixed factor despite it being non-significant as this is an important factor that could influence entropy.

2.3.7 Ethics

All work was conducted under Home Office license PPL 30/3204. Chicks were kept in less densely populated conditions than is recommended by DEFRA's code of practise (DEFRA, 2010) to reduce stress and all task participation was voluntary.

2.4 Results

2.4.1 Did the birds learn the spatial tasks?

Performance improved as trial number increased in all both spatial cognition tasks, while sex, test order and body mass had no effect (Table 2.1). Birds improved on the Top-Bottom task from a mean performance (chance of choosing correctly) of 0.293 [95% CI: 0.147-0.438] on their first trial to 0.854 [0.741-0.967] on the final trial (trial 50:X50) (Figure 2.5a).

In the cup task, errors reduced from a mean of 2.244 [1.676-2.812] in the first trial to a mean of 0.927 [0.593-1.261] in the final trial (trial 6) (Figure 2.5b). Birds made more consecutive zero-error trials (mean [95% CI] = 2.000 [1.532-2.468]) than expected by chance (mean [CI] = 1.128 [1.126-1.130]. Specifically, fewer birds had 0 (real = 3, simulated mean [CI] = 7.264 [7.216-7.312]), 1 (real = 19, simulated mean [CI] = 23.800 [23.739-23.862]) or 2 (real = 6, simulated mean [CI] = 7.853 [7.804-7.902]) consecutive zero error trials than expected by chance, whereas more birds had 3 (real = 4, simulated mean [CI] = 1.668 [1.643-1.693]), 4 (real = 7, simulated mean [CI] = 0.344 [0.332-0.355]) 5 (real = 1, simulated mean [CI] = 0.061 [0.056-0.066]) and 6 (real =1, simulated mean [CI] = 0.010 [0.008-0.012]) consecutive zero-error trials then expected by chance (Figure 2.6).

Table 2.1 Generalized linear mixed model output for binomial error and logit link function (Task 1) and Poisson error with log link function (Task 2). * denotes present in final model. Subscript numbers are rank of removal according to stepwise drop term model selection. Statistics are given for the model in which the variable was removed or for the final model.

n = 41	**Estimate**	**SE**	**χ^2 statistic**	***P***
Top-Bottom Task				
Sex[1]	0.029	0.349	0.007	0.934
Mass[2]	-0.145	0.143	1.027	0.311
Test Order[3]	-0.128	0.120	1.109	0.292
Trial Number*	0.468	0.051	89.483	<0.001***
Cup Task				
Test Order[1]	0.002	0.111	0.001	0.974
Mass[2]	-0.121	0.111	1.161	0.281
Sex[3]	0.231	0.162	1.955	0.162
Trial Number*	-0.295	0.057	27.161	<0.001***

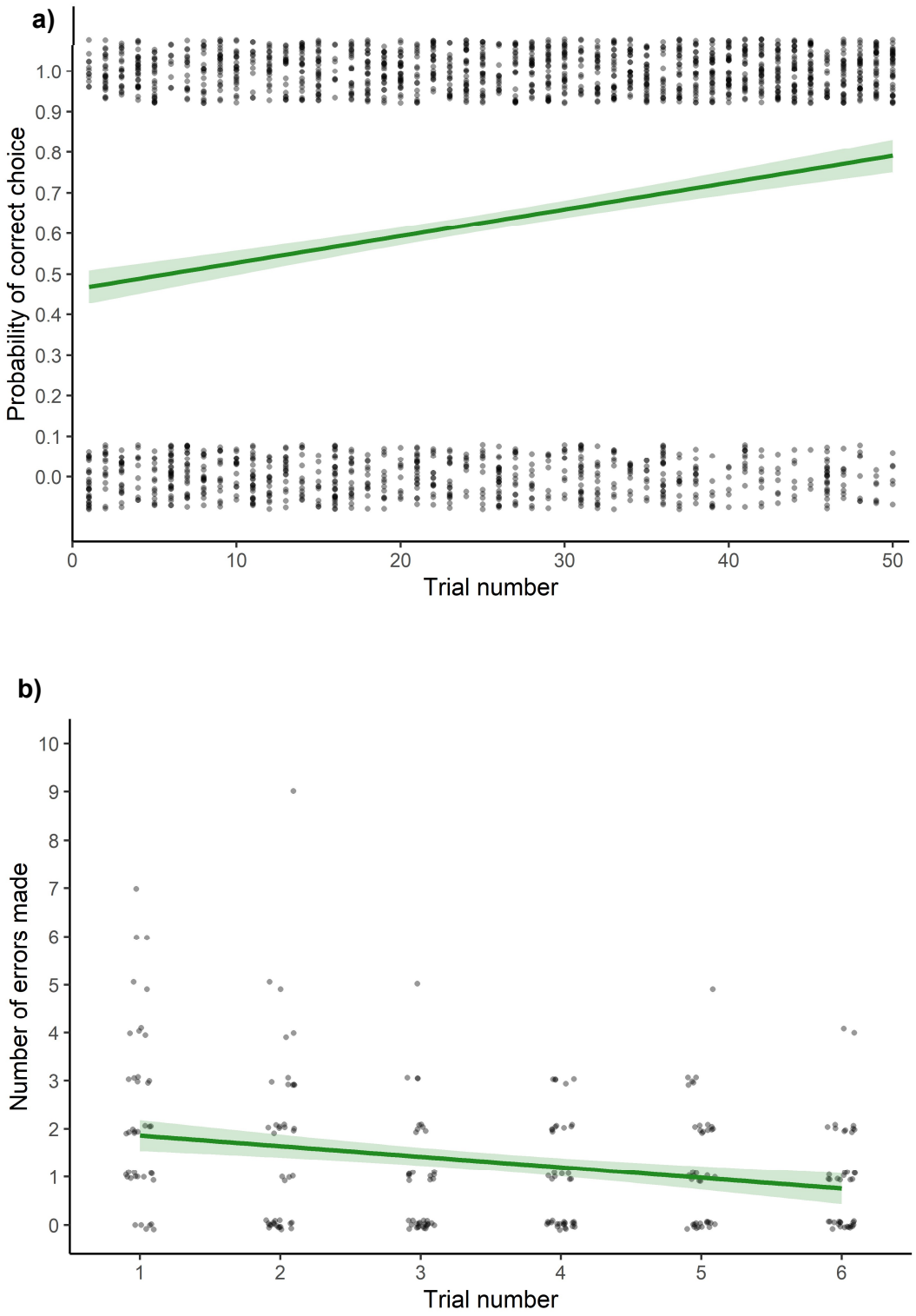


Figure 2.5 Performance of pheasants on the a) Top-Bottom task and b) Cup task. Black circles denote raw data where 0 = incorrect choice and 1= correct choice in each trial. Points have been spread to allow for visualisation of the density of points. Green lines denote model prediction with 95% confidence intervals.

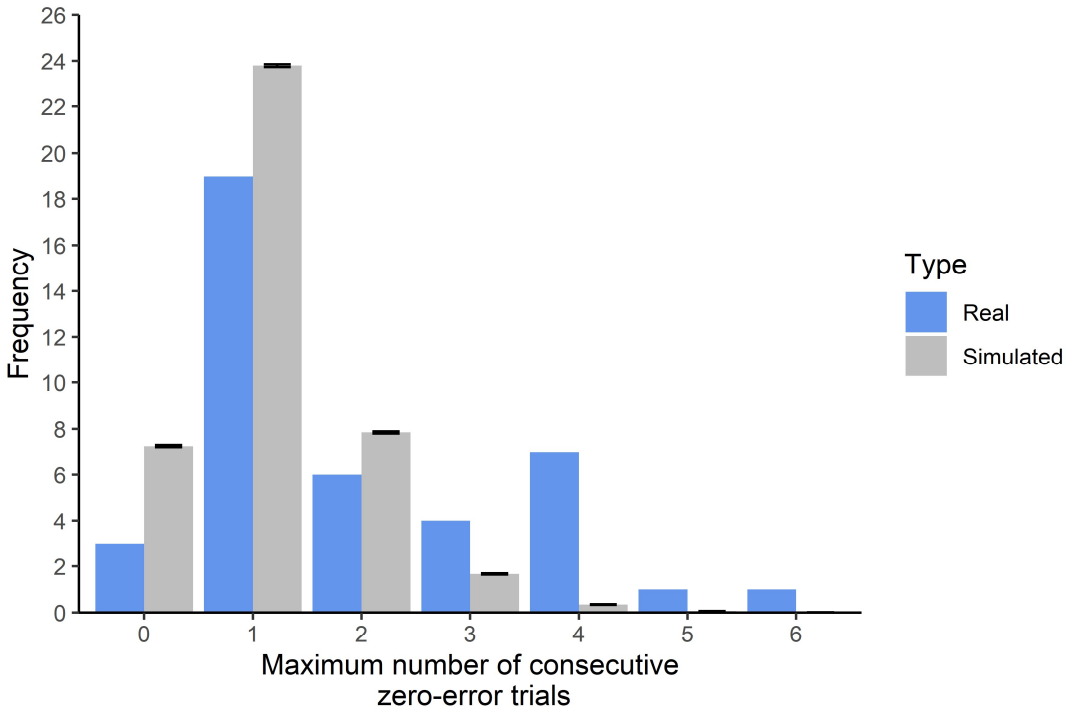


Figure 2.6 Distribution of scores for the cup task (blue) in comparison to the expected distribution (grey) where each bar represents the mean expected frequency of each score from a simulation of 10,000 iterations of 41 simulated individuals, each with 25% chance of a correct first choice for each trial. Error bars are 95% confidence intervals for each score over the 10,000 iterations.

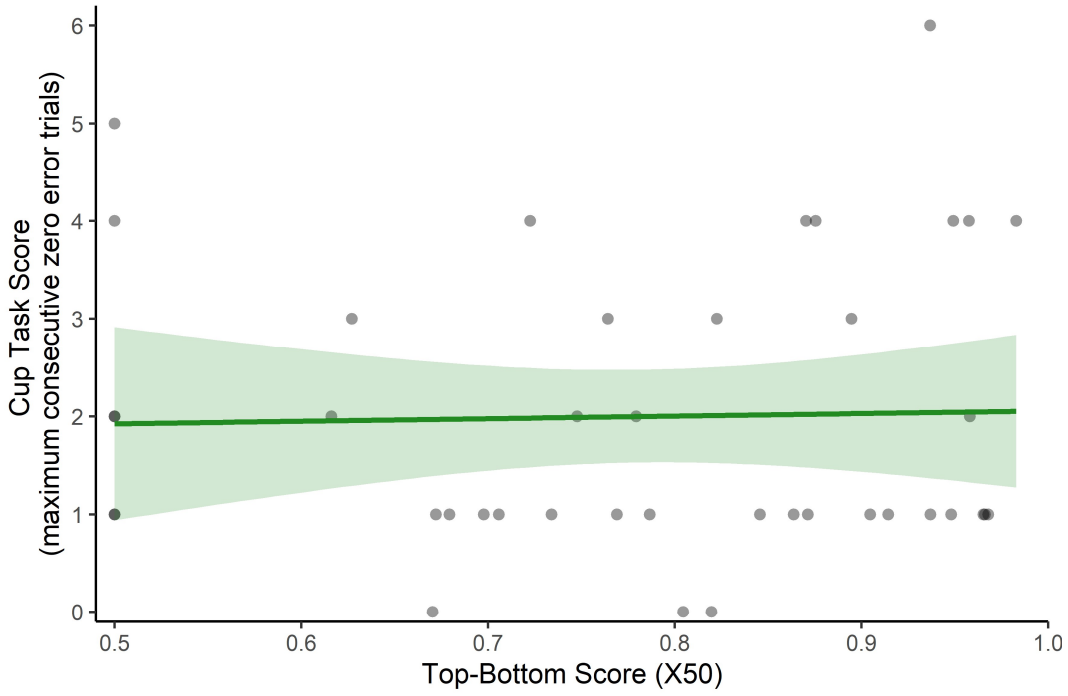


Figure 2.7 Scatterplot to demonstrate the distribution and relationship between the two spatial tasks. Green line is a regression line with 95% confidence intervals.

2.4.2 Are pheasants consistent in their performance across 'spatial' cognitive tasks?

Task performance on the small-scale spatial task (Top-Bottom) and the larger-scale spatial task (Cup task) did not correlate (R = 0.032, n = 41, p = 0.842, Figure 2.7).

2.4.3 Do cognitive or non-cognitive factors influence diversity of feeder use?

Diversity of feeder use, calculated as entropy, ranged from 0.293 (preferred feeder = 13 visits, 2nd feeder = 1 visit) to 1.433 (preferred feeder = 7 visits, 2nd feeder = 5 visits, 3rd Feeder = 4 visits, 4th Feeder = 4 visits) and had a mean value of 1.09 (example entropy = 1.094: preferred feeder = 10 visits, 2nd feeder = 5 visits, 3rd feeder =1 visit, 4th feeder = 1 visit) (Figure 2.8). Birds with better performance on the Top-Bottom task had a higher feeder diversity and therefore

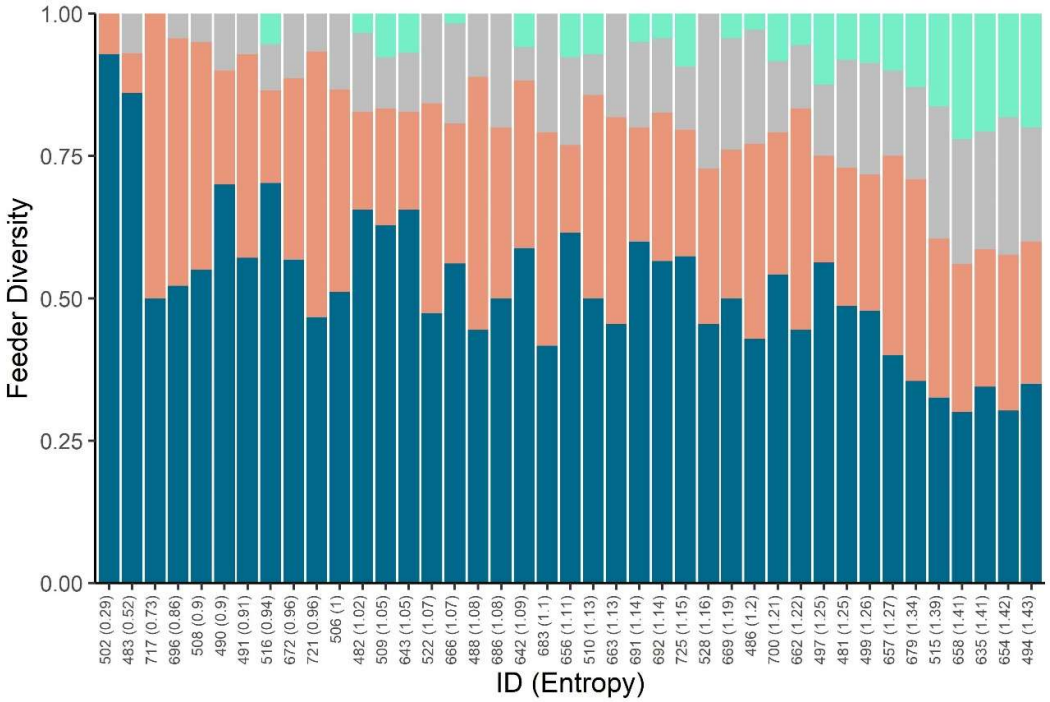


Figure 2.8 Feeder diversity of all 41 individuals. An individual's most frequently used feeder is shown in dark blue, secondary feeders are shown in orange, grey and green according to respective usage. Individuals are ordered from least diverse (lowest entropy) on the left to most diverse (highest entropy) on the right.

used the space more evenly than birds that performed poorly on the task (Table 2.2, Figure 2.9). There was no effect of any other cognitive or non-cognitive traits on the diversity of feeder use. We noted two outliers that had high Top-Bottom task performance but low entropy (Figure 2.9). These individuals were identified as only being present for 3 days (although they meet the criteria of at least 8 visits and were therefore included in the analysis). All other birds attended feeders for over three days but removing these two individuals does not change the outcome of our analysis therefore we kept them in the analysis.

Table 2.2 General linear model output. * indicates presence in final model. Subscript numbers are rank of removal according to stepwise drop term model selection. Statistics are given for the model in which the variable was removed or for the final model.

N=41	Estimate	SE	F statistic	*P*
Sex[1]	0.005	0.102	0.002	0.959
Mass[2]	0.012	0.039	0.102	0.752
Test Order[3]	-0.020	0.034	0.359	0.553
Cup Task Score[4]	-0.048	0.033	2.143	0.152
Total Number of Visits*	0.029	0.032	0.794	0.378
Top Bottom Score*	0.092	0.032	8.187	0.007**

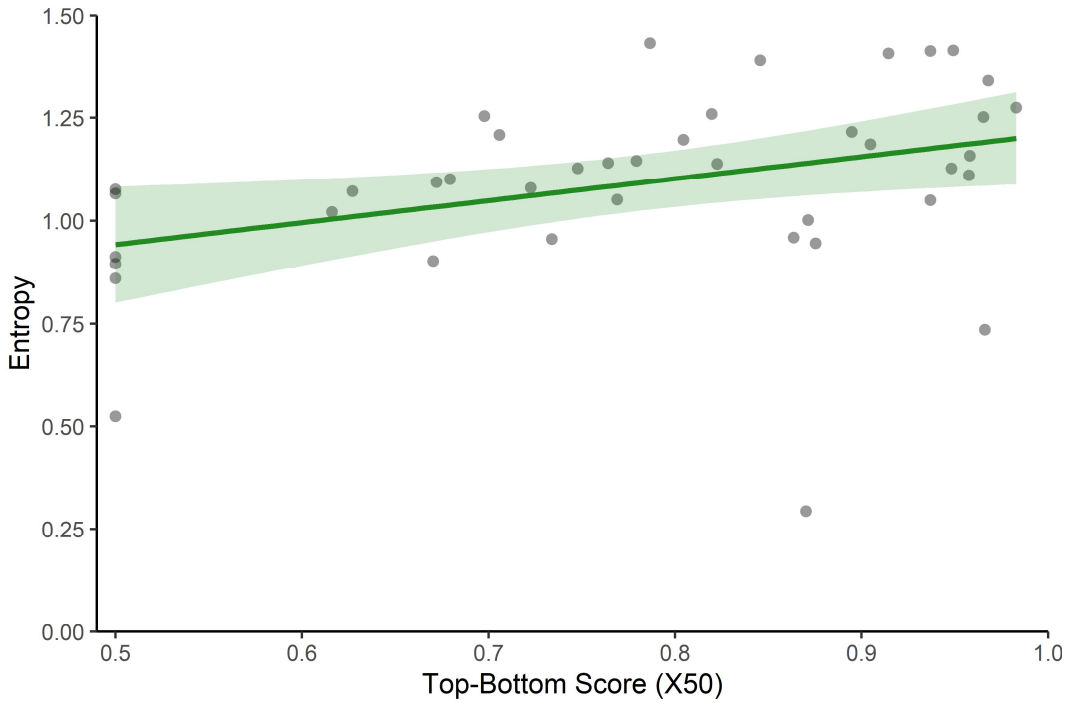


Figure 2.9 Model prediction for final model showing that higher scores on the Top-Bottom task predicts higher diversity of feeder use. Raw data are plotted as black circles.

2.5 Discussion

Pheasants show inter-individual variation in their foraging patch diversity in a semi-natural, restricted area, despite all feeder stations having *ad libitum* food availability. This variation is related to individual differences in spatial cognitive ability in a small-scale but not a large-scale spatial task, indicating that spatial cognition may play a subtle role in fine scale foraging decisions which help to explain broad-scale space use. Individuals that performed better on a small-scale binary spatial discrimination task used four foraging patches more evenly and therefore had higher foraging patch diversity than conspecifics. However, performance on a larger-scale foraging task bore no relationship to subsequent diversity of foraging patch use. This is possible because an individual's performance on the spatial tasks were unrelated to one another.

The lack of correlation between the spatial tasks could indicate that we may have measured distinctly different cognitive processes in each task; that we did not measure cognitive processes in one or both tasks; or that performance on spatial tasks is not repeatable within individuals over different contexts or across time. The most salient difference between these two tasks is their scale and this feature has previously been shown to explain differences in spatial abilities between sexes within a species. For example, female brown-headed cowbirds (*Molothrus ater*) outperformed males in a large scale spatial task (scale: 180 cm X 180 cm) but this effect was reversed in a smaller scale spatial task (scale: 8.5 cm X 8 cm) (Guigueno et al., 2015, 2014). This may indicate that different processes underlie each task type, and that the cognitive processes involved in solving the Top-Bottom task are most relevant to fine-scale foraging decisions. However, it may

also be that the Top-Bottom task simply provided the most coherent learning opportunity. We conducted 50 trials for the binary choice tasks as opposed to 6 trials in the cup task. This difference was due to logistical challenges, namely that birds could perform multiple binary choices while in the same test session but were required to leave the testing chamber to perform further cup task trials. To keep stress to a minimum we only performed a maximum of two sessions per day, which limited the amount of trials we could conduct. While six individuals failed to learn the Top-Bottom task, twenty-two birds failed to perform two or more consecutive zero-error trials. To capture individual differences within the cup task we therefore may have needed to conduct more trials to robustly measure variation in performance.

Although cognition is often assumed to play a role in site fidelity (Irons, 1998), to our knowledge, no studies have explicitly linked individual variation in spatial cognitive ability to variation in foraging site fidelity or the relative diversity of sites used. Young pheasants that performed better on a small-scale binary spatial discrimination task utilised a higher diversity of feeders within a restricted area, where all birds had access to the four 'unlimited' feeder stations of the same type of forage. Therefore, for pheasants, it appears that individual variation in diversity of patch use is linked to individual differences in spatial cognitive ability. Feeder diversity varied with some individuals almost exclusively using one feeder whereas others exhibited relatively equal usage across four feeders. This feeder usage could be representative of the spatial scale of movement within the pen where equal usage may indicate that birds used more space within the enclosure. This links to previous work whereby better performance on spatial tasks has been shown to correlate positively with larger ranges occupied by males in some

polygynous species (e.g. meadow voles, *Microtus pennsylvanicus* (Gaulin & Fitzgerald, 1989) and giant pandas, *Ailuropoda melanoleuca* (Perdue et al., 2011)). In these species, sex differences may have evolved in proportion to navigational demands. Despite pheasants displaying sex differences in movement patterns from an early age (Hill & Ridley, 1987), we did not find any difference in either spatial cognitive ability in any of our tasks or diversity of feeder use between the sexes. Both of these previous studies linked spatial tasks that were more representative of our cup task (in requiring ambulation to complete a task) rather than a small-scale task. However, the measure of spatial scale in these studies was adult home range, whereas we measured foraging site use as juveniles and during the first ten days since their introduction into a relatively small area (4000 m^2). We did this to control for individual experience and the availability of different landscape features that could be used for navigation. However, different spatial cognitive processes may be important for different types of space use and life stages, which could explain why only our small-scale spatial task explained variation in foraging patch use.

Other behavioural phenotypes such as personality i.e. exploratory behaviour (Fisher, James, Rodríguez-Muñoz, & Tregenza, 2015) or boldness (Harris et al., 2020) could also be an important explanatory factor that we did not account for in this study. For instance, more exploratory individuals may lead to using more feeders as a consequence of increased movement (Spiegel, Leu, Bull, & Sih, 2017). Social factors could also be an important influence on feeder usage (Hintz & Lonzarich, 2018). While the content of each feeder was the same, both affiliative and agonistic social interactions could have influenced attendance at particular feeders, modifying the perceived value of each feeder at the individual

level. Greater diversity in feeder use may indicate that an individual was especially vulnerable to intraspecific competition at feeders and so was driven from one to another (if small or subordinate) or could monopolise a single feeder itself (Svanbäck & Bolnick, 2007). However, we found no evidence that mass, sex or test order had any effect on feeder diversity, which may be expected if competition had excluded smaller or less motivated individuals.

Better spatial cognitive ability, as indicated by performance in the Top-Bottom discrimination task best explains the variation in feeder diversity that we observed. Resources can be more efficiently exploited if an individual encodes locations of profitable areas to memory (Van Moorter et al., 2009). Better spatial cognitive ability could permit individuals to move between resources already encoded in memory, when the value of a resource declines. Because our feeders provided 'unlimited' food, and the birds were protected from terrestrial predation at the feeders, a decline in value is unlikely although individual perception of value may differ according to external influences such as social factors. It seems that those with better spatial memory resample more foraging patches that their poor performing counterparts. We found poor relationships between an individual's performance across our battery of 'spatial' tasks, highlighting the importance of conducting multiple tasks. Despite this, our work provides encouraging, and rather rare, evidence that cognition is an important determinant of the fine-scale foraging decisions that can ultimately lead to broad-scale space use.

3 Daily patterns of foraging onset are repeatable and have survival implications, but are not driven by cognitive factors.

3.1 Abstract

In many diurnal species, peaks in foraging behaviour occur in the early morning to compensate for energy use and fasting during the night. However, the mechanisms that underlies the onset of foraging have received little attention. Spatial cognitive ability may play an important role in determining when an animal first arrives at foraging patches, potentially giving options of more efficient routes between patches and/or sleeping sites. We assessed the spatial cognitive ability of pheasant chicks, *Phasianus colchicus,* using a binomial spatial discrimination task and a larger scale 2 x 2 foraging grid. We considered whether scores on these tasks, along with non-cognitive factors, specifically, a measure of food motivation (rank order to enter testing chamber and obtain rewards), body size and sex influenced the order at which birds began foraging in the wild and the number of days survived. Pheasants were fitted with a PIT tag and then released into an agricultural landscape. The landscape contained 43 fixed supplementary feeding sites fitted with RFID readers and we monitored the time and order of pheasants' arrival at them. The order in which birds arrived at foraging sites was repeatable (R=0.144) but was not predicted by an individual's spatial cognitive ability, sex or motivation. Instead, we found that larger birds arrived at feeders before smaller birds. Survival probability was lowest for birds that arrived later and for male pheasants. This study presents a complex interaction of sex, body size and foraging decisions that has consequences for an individual's chances of survival, but spatial cognitive ability does not seem to play a role.

3.2 Introduction

The decision of when to leave a refuge and begin foraging is an important one. For many diurnal prey species, the onset of foraging behaviour coincides with leaving a safe refuge and commencing a trade-off between foraging and predation risk (Lima & Dill, 1990). Emerging earlier from a refuge than conspecifics has been shown to increase mortality in goldfish, *Carassius auratus* (Balaban-Feld et al., 2019) and under high predation risk, some species will delay the onset of foraging (e.g. dark eyed junco, *Junco hyemalis*, (Lima, 1988) or great tits, *Parus major* (Krams, 2000)), presumably because predation risk is higher in dimmer light conditions (Cerri, 1983). However, while variation in the timing of emergence exists at the population level, this may be driven by consistent individual-level differences (e.g. in great tits, *Parus major* (Stuber et al., 2015) and blue tits *Cyanistes caeruleus* (Steinmeyer, Schielzeth, Mueller, & Kempenaers, 2010)), indicating that some individuals may consistently express riskier behaviour than others. The mechanisms underlying these differences are unclear. Differences in foraging onset may arise due to differences in personality traits, with bolder individuals arriving first at foraging locations (Kurvers, Nolet, Prins, Ydenberg, & Van Oers, 2012), hunger levels (Morgan, 1988; Whitham & Mathis, 2000), linked to consistent differences in metabolic rate (Biro & Stamps, 2010) or underlying circadian mechanisms (Helm et al., 2017). One important, yet unexplored, explanation is that foraging onset is influenced by an individual's ability to collect, store and utilise spatial cognitive information (hereafter spatial cognitive ability).

Cognitive abilities differ between individuals (for reviews see Boogert, Madden, Morand-Ferron, & Thornton, 2018; Thornton & Lukas, 2012) and are suggested to be critical in determining individual movement patterns (Fagan et al., 2013; Nathan et al., 2008). Specifically, memory of the spatial environment is assumed to influence movement path structure between refuges and foraging patches, with paths becoming more direct as experience increases over time (Carter et al., 2019; Osborne et al., 2013), reducing the time spent in transit. If animals emerge from refuges primarily to forage, then the time spent moving between a refuge and foraging patch should be minimised to limit energy expenditure and maximise the time available to forage. Spatial cognitive ability could influence time of arrival at foraging sites in one of three ways. First, individuals may remember safer routes, so that predation risk associated with earlier emergence from a refuge could be offset, enabling them to begin moving to foraging sites earlier, in dimmer light conditions. Second, individuals may be able to navigate more effectively in low light when landmarks are obscured and again, begin moving to foraging sites earlier. Finally, individuals may remember quicker or more direct routes to foraging sites and so arrive earlier relative to birds with poor spatial cognitive ability. In all cases, individual's with better spatial cognitive ability may arrive sooner and so increase their foraging time.

The timing of arrival at foraging sites may have fitness consequences for an individual, and therefore selection may act upon individual attributes that determine the onset of foraging, including spatial cognitive ability. Most importantly, early arrival at foraging sites may influence the probability of survival. This may operate indirectly, with individuals that consistently begin foraging earlier being able to forage for longer, thus gaining higher energy reserves and

longer survival duration in harsh conditions (Ekman & Hake, 1990). There may also be direct effects with individuals that begin foraging consistently earlier than others facing increased risk of encountering predators, either because foraging times overlap with nocturnal or crepuscular predators which are still active in the early morning (Caravaggi et al., 2018), or because predators pose greater risk under poor light conditions (Cerri, 1983). Therefore, we might expect that there are optimal times for foraging onset by each individual that maximises their survival, and these may be subtle (e.g. rates of food intake), or more obvious (e.g. survival through reduced encounters with predators).

Temporal aspects of foraging patterns have been of interest at the population level for decades (Alanara, Burns, & Metcalfe, 2001; Fitzpatrick, 1997; McNamara, Houston, & Lima, 1994; McNamara, Mace, & Houston, 1987; Pagani-Núñez & Senar, 2013) but only recently has empirical work concentrated on the interplay between ecology and circadian patterns (Helm et al., 2017). Studies investigating temporal patterns of foraging behaviour at the individual level are relatively rare. Temporally mediated foraging strategies such as the frequency and duration of foraging behaviour has been shown to be repeatable within individuals (Moiron et al., 2018). Further to this, in great tits and blue tits, the time of foraging onset has been shown to be related to these foraging strategies, with birds that make fewer but longer foraging bouts also beginning foraging later in the day (Milligan et al., 2017). Other circadian behaviours such as time of awakening, rest onset and rest duration within pearly razorfish *Xyrithchys novacula* (Alós, Martorell-Barceló, & Campos-Candel, 2017) as well as sleep and refuge-exiting behaviour in great tits (Stuber et al., 2015) and blue tits (Steinmeyer et al., 2010) have been found to be repeatable within an individual,

indicating that robust, individual chronotypes (behavioural manifestations of an individual's internal clock) may exist. However, to our knowledge, the consistency of an individual in initiating daily foraging has not yet been assessed despite its perceived importance in the starvation-predation trade-off (Lima & Dill, 1990). To determine whether the onset of an individual's foraging behaviour is influenced by their cognitive ability (or any other fixed inherent factor), it is first necessary to demonstrate that the timing of the onset of foraging is repeatable.

Measuring individual differences in spatial cognition is not a trivial task (Völter et al., 2018) and must be inferred through performance on behavioural tasks that require spatial information to be remembered. For non-human animals, these tasks frequently constitute foraging problems, whereby food is hidden in a specific location within an area. The area may constitute a grid of potential locations (Saleh & Chittka, 2007; Sulikowski & Burke, 2010; Sutherland & Gass, 1995); an open ring or square array (Croston et al., 2016; Perdue et al., 2011) or a radial maze (Olton & Samuelson, 1976). Tasks of different spatial scales may measure different aspects of spatial cognition and have been shown to be uncorrelated in previous studies (Guigueno, Macdougall-Shackleton, & Sherry, 2015; Sauce et al., 2018; Chapter 2), although it is as yet unclear why these differences occur. While it is possible to assess spatial cognitive ability in the wild (e.g. Shaw, Boogert, Clayton, & Burns, 2015; Sonnenberg, Branch, Pitera, Bridge, & Pravosudov, 2019), it is helpful to assay cognitive abilities early in life, with individuals at comparable experience levels, since age (Begega et al., 2001) and prior experience, facilitates access to information, (Clayton, 1995; Clayton & Krebs, 1994a) and can influence an animal's performance in spatial tasks. Furthermore, experience about the environment can also influence risk-taking

behaviour (Frost, Winrow-Giffen, Ashley, & Sneddon, 2007), therefore it is also desirable to monitor foraging decisions from first encounter with the environment when all individuals are naïve to conditions and each possess the same level of information about the risks and rewards available.

We investigated whether individual pheasants', *Phasianus colchicus,* onset of foraging at artificial feeders in a natural landscape could be explained by their spatial cognitive ability, controlling for potentially influential non-cognitive factors and whether this influenced their survival. Pheasant chicks can be reared in large numbers in standardised conditions. Furthermore, chicks can easily be habituated to take part in a range of cognitive and non-cognitive tests during this captive period (Madden, Langley, et al., 2018; van Horik, Langley, Whiteside, Beardsworth, et al., 2018; Whiteside, Bess, et al., 2018), and provide an already established system for the study of spatial cognition (Langley, van Horik, Whiteside, Beardsworth, & Madden, 2018; Langley, van Horik, Whiteside, & Madden, 2018b). Crucially, in the UK, pheasants are released into the wild to supplement hunting stock where they are subject to natural selection pressures. Released pheasants are provided with supplementary food at fixed locations in the form of grains from feeders. Birds visiting such feeders can be monitored by PIT/RFID technology (see also Aplin, Farine, et al., 2013; Aplin, Sheldon, & Morand-Ferron, 2013; Firth, Voelkl, Farine, & Sheldon, 2015).

Foraging onset is likely to depend on predation risk (Krams, 2000; Lima, 1988). The primary predator of the pheasant, the red fox, *Vulpes Vulpes* (Madden, Hall, & Whiteside, 2018; Robertson, 1988) is a nocturnal and crepuscular generalist

carnivore (Caravaggi et al., 2018) and although they can be active during the day, they will often avoid diurnal periods (Baker, Dowding, Molony, White, & Harris, 2007; Cavallini & Lovari, 1994; Doncaster & Macdonald, 1997), despite increases in prey abundance (Díaz-Ruiz, Caro, Delibes-Mateos, Arroyo, & Ferreras, 2016). Predation risk for pheasants is therefore likely to be high in the very early morning when pheasants leave their sleeping site and move to a foraging site. We predict that better spatial cognitive ability will benefit pheasants by enabling them to begin foraging sooner and allowing them more time to accumulate the resources needed for the day.

Foraging onset is also likely to depend on energy demands, which increase with body size (Kendeigh, 1970; Peters, 1983). Pheasants are sexually dimorphic in size from 3 weeks old (although there is some overlap) (Whiteside, van Horik, Langley, Beardsworth, & Madden, 2018) and sex differences have been reported in both spatial and temporal foraging behaviour (Whiteside et al., 2019). Whiteside et al. (2018) showed that males tend to forage early in the morning and in the afternoon and females are present at feeders during mid-morning, therefore we expect population level variation in the onset of foraging. However, whether individual males forage at both early morning and afternoon or if individuals only utilise one time period is unclear. While body mass may provide one indication of energy demands, a second indicator may be motivation to access food rewards. Previous work has found that found that pheasants are repeatable in their order of (voluntary) entry into a testing chamber during cognitive testing (van Horik et al., 2016). This may be a measure of motivation to attain food rewards. We expect birds with larger body mass and thus higher energy requirements and/or

individuals that were more highly motivated to enter our testing areas to start foraging earlier, either absolutely or relative to one another.

The timing of foraging onset may have fitness consequences for individual pheasants. Indirectly, timing of foraging may affect their food intake and thus alter their body mass, which has been shown to be positively related to survival (Dumke & Pils, 1973), with birds starting to forage at suboptimal times achieving a lower food intake. Foraging onset may directly expose pheasants to predators, such that individuals starting to forage at suboptimal times are more likely to be killed. Good spatial ability may enable pheasants to remember better, perhaps safer routes, therefore decreasing predation risk. Pheasants are large and conspicuous and we can monitor their survival through direct searches, radio tracking or noting their absence from direct observations or camera traps (Robertson, 1988; Snyder, 1985; Turner, 2007; Whiteside, Sage, et al., 2016). Therefore, we used mortality as a fitness measure and test whether there were optimal foraging onset times that reduced the probability of death for an individual.

We explored the causes and consequences of the temporal foraging decisions of young pheasants. To do this, we first measured the extent to which pheasants were repeatable in their daily arrival times and the order of arrival at foraging sites. Next, we assessed the factors that we predicted might influence the onset of foraging behaviour such as spatial cognitive ability, motivational traits, release day mass and sex, against the rank order of arrival of birds at feeding stations. To assess potential consequences of these decisions, we also monitored their

fate and retrospectively assayed mortality risk by conducting a survival analysis. If spatial cognitive ability is an important determinant of an individual's temporal foraging patterns then we would predict that such ability, as indicated by performance in tests of spatial cognitive ability, would explain a significant portion of the variance in the onset of foraging behaviour. If relative safety of routes, rather than simply the efficiency of routes, is key to earlier onset of foraging behaviour then we would expect survival probability to be linked to an interaction between the onset of foraging and spatial cognitive ability.

3.3 Methods

3.3.1 Subjects and Housing

One hundred and ninety-seven pheasant chicks were housed in one of four identical (1.75 m x 2 m) indoor heated enclosures (3 x 50 chicks, 1 x 47 chicks) from one day old between 19th May and 21st July 2016 at North Wyke Rothamsted Research farm (Devon, 50º77'N, 3º9'W). The birds in two of these enclosures (the enclosures that were given spatial tasks) are the same birds as were used in Chapter 2. Birds were given *ad libitum* access to commercial chick crumb (Sportsman Game Feed), water and had access to perches. At 4 weeks old, birds were able to enter an outdoor, grass run (4 m x 12 m) that contained extra feeders, drinkers and perching. Within the indoor enclosure, but separated by a sliding door, was a testing chamber (0.75 m x 0.75 m) and through which birds could pass into the post-testing area (Fig. 3.1). A mesh partition could be lowered and raised to separate pre- and post- testing areas within the indoor enclosure.

3.3.2 Cognition Tasks

We presented birds in two of the enclosures (n = 100) with two extractive foraging tasks to assess their spatial cognitive ability. Birds in the other two enclosures were used for a different experiment and so could not be included in our analyses of what factors influenced foraging onset, but they were released at the same time and were therefore included in the repeatability and survival analyses. After an initial training period, we gave birds one small scale spatial task (binary discrimination) and one large scale spatial task (cup task). We gave tasks to the birds in the same order across pens to control for potential effects of age and experience as the birds developed.

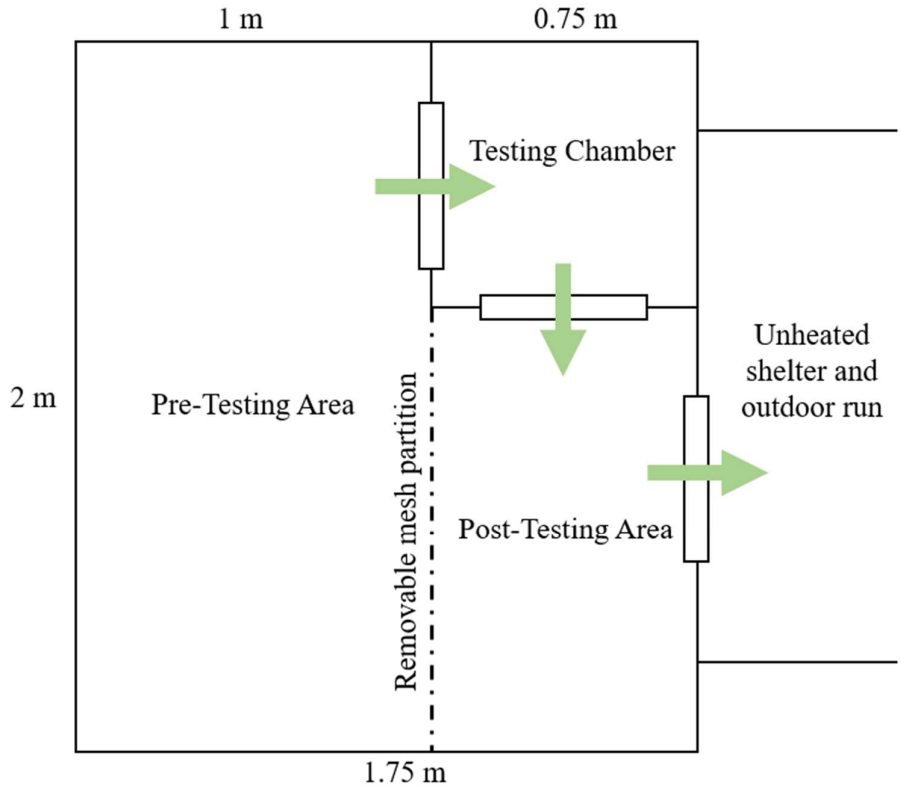


Figure 3.1 Schematic of indoor enclosure. For testing periods, the removable mesh partition is lowered to separate pre- and post-testing areas. Birds enter the testing chamber from the pre-testing area to complete cognitive tasks then enter the post-testing area where they can also gain access to outside (arrows show the route).

3.3.2.1 Training

We shaped all birds to enter the testing chamber using mealworm rewards until they entered the chamber alone and voluntarily with no obvious visual indicators of stress. Our first training apparatus consisted of a 45 cm x 15 cm white box (hereafter poke box) which contained 10 (2 x 5 array) wells (2 cm diameter x 1.8 cm deep). We first trained birds to peck through crepe paper covering wells to retrieve a mealworm reward and mealworms were available in every well. After this initial training, birds needed to 'unlearn' that every well was rewarded to effectively learn spatial cues (as opposed to learning both spatial cues and the consequences of incorrect choices). We therefore trained birds to solve a small-scale binary discrimination task (Left-Right, see Chapter 2 for more details),

where the birds were given only one choice and one reward (right well) per trial. This used the same size poke box but in a 1 x 2 array of wells in the centre of the box. Each bird received 50 training trials (10 trials per session over 5 sessions) between 9 am and 2 pm on the 6th - 7th June 2016 and at 9 am on the 8th June 2016.

3.3.2.2 Small Scale Task: Top+ Bottom- Binary Choice

We assessed an individual's ability to learn small-scale (smaller than the bird's body size) spatial discriminations by presenting them with a choice of two wells in which the top well was always rewarded whereas the bottom well was always unrewarded. The wells were a rotated (90 º) version of the training binary discrimination which we presented in a 1 x 2 array, whereby one well was situated closer to the bird (bottom well) and the other was farther away (top well) with a 1 cm gap between wells. We placed a visible mealworm between the two wells to centralise the bird at the beginning of each session. The second, and subsequent, trials were presented immediately after the bird had made a choice between the two wells and retrieved the reward (if applicable). As in the training sessions, each bird was given 10 trials over 5 sessions with testing starting at 2 pm on the 8th June 2016 and at 9 am and 2 pm on the 9th - 10th June 2016. Ninety-nine individuals completed all 50 trials of this task.

We generated learning curves using generalized linear models (family= binomial, link function = log) to predict an individuals' probability of choosing correctly in their final (50th) trial. This probability was used as their score in this task for subsequent analysis.

3.3.2.3 Large Scale: Cup Task

At 5 weeks old, we assessed an individual's ability to learn and remember large-scale (larger than the bird's body size) spatial cues using a foraging grid. We placed four plastic cups at each corner of the testing chamber, situated ~50 cm apart. Birds were lured to the centre of the chamber using a clearly visible mealworm. We placed a mealworm reward (3 mealworms) in the cup that was both furthest from the entrance door and closest to the experimenter. The reward inside the cup was not visible to the bird until they inspected the interior of the cup. Choices were determined as approaches within 12 cm (~1 body length) of any cups. The number of incorrect choices made before the bird retrieved the reward was recorded and the birds completed 6 sessions between 21st-24th June 2016. The maximum number of consecutive, zero-error trials was defined as the birds score on this task. Ninety-two birds completed all six trials for this task.

3.3.2.4 Motivation

Individuals voluntarily entered the testing chamber and the order in which pheasants entered has previously been found to be repeatable (van Horik & Madden, 2016). It is not clear whether birds that enter earlier are more dominant, more motivated to receive a reward or conversely more keen to remove themselves from conspecifics. However, we frequently observed several individuals defending the entrance to the testing chamber and despite this behaviour, other birds would attempt to pass these birds to enter the testing chamber and access the high value mealworms. Therefore, we suspect that food motivation is the primary factor influencing test order. More motivated individuals therefore have a lower median test order overall. The median test order of 24

testing sessions (including one other task not used in this study) was calculated for each bird and used as a score of motivation.

3.3.3 Release

When the pheasants were 10 weeks old (21st July 2016), we sexed (via plumage), weighed (using a Samson spring balance - precision 5 g) and attached leg-ring PIT tags to all individuals before releasing them into an open-top release pen (~4000 m^2) situated within a wooded area at our field site (see Chapter 2). Forty-three barrel-feeders containing a mix of chick crumb and wheat were placed around the farm (as in Whiteside et al., 2019) permitting *ad libitum* feeding within and outside the pen.

3.3.4 Measuring Foraging Behaviour

To monitor foraging bouts, RFID readers comprising a custom flat aerial (35 cm diameter) covered with artificial grass, attached to an IB Technology logger) were situated underneath each feeder to log visits from birds, scanning for tags at 1 second intervals.

We determined when an individual first foraged at supplementary feeding sites using two measures extracted from the data. First, for each day, we extracted the first time point that an individual visited their first feeder (total = 6052) and from this calculated the time lag in minutes between this and civil dawn. Secondly, for each day, we ranked individuals by the time that they visited their first feeder in

efforts to remove any effects that environmental and social factors could have on timing. We chose the most repeatable measure for further analyses.

3.3.5 Survival

We assessed survival probability retrospectively, by monitoring activity of birds at feeders until 1st March 2017 and actively conducted detailed searches for corpses within our field site for the first 90 days post release. Birds that were found dead were assigned a cause of death using field signs. It is important to note that although field signs may suggest predation, the bird itself could have died of other causes and was then scavenged. Any birds that had been shot on nearby game shoots could also be reported to us through a phone number found on the patagial wing tags. While we do not consider shot birds as predated, we included these birds as censored but alive on the day they were shot (n = 1 15th Dec 2016; n = 3 5th Jan 2017) as they were shot close to the end of the tracking period and this was indicative of a longer survival period.

3.3.6 Statistical analysis

All analysis was conducted in R v3.6.1 (R Core Team, 2019) using RStudio (RStudio Team, 2018) as a wrapper. Figures were created using *ggplot2* v3.2.0 (Wickham, 2016).

The number of birds available to assess foraging behaviour reduced rapidly as individuals dispersed from the field site or were predated. We therefore kept all foraging analysis to a period of one month post release (23rd July – 31st August

2016) to maintain maximal sample size and keep foraging patterns comparable because of potential differences in food availability and day length across the season (McNamara et al., 1994). Of the 197 birds released, we detected 173 birds at feeders at least once during the study period.

3.3.6.1 Did birds learn the spatial tasks?

We tested, at the population level, if the chicks improved performance in the spatial tasks as trials progressed using generalised linear mixed models (GLMM) (*lme4* v1.1-15) (Bates et al., 2015). For the binary choice task, we fitted a GLMM with a binomial error structure and a logit link function with choice (0 = incorrect, 1 = correct) as the response variable and trial number (1-50), body mass (on release day), sex and median test order as a fixed effects. Each of the fixed effects were continuous therefore we scaled and centred them using the *scale* function in base R. For the cup task we fitted GLMM with a Poisson error structure and log link function. Number of errors (per trial) was used as the response variable and again trial number (1-6), body mass and median test order were scaled, centred and fitted as fixed effects. For both models we accounted for repeated observations of individuals by adding bird ID as a random effect. We reduced the model to the minimum model using backwards stepwise deletion through the *drop1* function in base R and chose the model with the lowest AIC.

3.3.6.2 When did pheasants forage?

We monitored the number of birds at any feeder across the field site within 15-minute periods to give a general overview of population level foraging activity.

3.3.6.3 Are foraging onset times repeatable?

For both timing and order of foraging onset, we calculated repeatability using GLMM-based repeatability estimation for Poisson distributed data using *rptR* v0.9.22 (Stoffel, Nakagawa, & Schielzeth, 2017). We estimated confidence intervals through bootstrapping (n = 1000).

3.3.6.4 What factors influence order of foraging onset?

We fitted a GLMM with a Poisson error structure and log link function to investigate whether order of arrival at feeders was influenced by performance on either top-bottom or cup task, body size (mass on release day), sex or test order. We included bird ID as a random effect. Backwards stepwise deletion was used to define the minimal model using *drop1* in base R.

3.3.6.5 Did order of foraging onset in conjunction with spatial cognitive ability influence survival?

We asked whether order of arrival at feeders predicted survival probability and if spatial cognitive ability influenced this by fitting two two-way interactions (the first between median order and performance on the top bottom task, and the second between median order and performance on the cup task) in a Cox's proportional hazards model (Therneau & Grambsch, 2000) using the *survival* (v2.44-1.1) R package (Therneau, 2015). Time1 was recorded as the number of days from release until their final detection at a feeder, live sighting, or the day they were shot, whichever was later. Birds whose fate was known were given a censored value of 1 (n = 34), all other birds were noted as uncensored and given a value of 0 (n = 134).

3.3.7 Ethical note

This work was approved by the University of Exeter Ethics Committee and conducted under Home Office license PPL 30/3204. To minimize stress during testing, all birds were habituated to humans from their first day of life and incrementally shaped to entering the testing chamber and engage with the test apparatus (in a group, then alone) using positive reinforcement only (mealworm rewards). Participation in all tasks was voluntary and food and water was available to all birds *ad libitum* except when they were participating in a task (maximum 3 minutes). Birds were reared at lower densities than recommended by DEFRA's code of practice, so it is assumed that this further reduced stress (DEFRA, 2010).

3.4 Results

3.4.1 Did birds learn the spatial tasks?

Performance improved as trial number increased in both spatial cognition tasks indicating learning of the task affordances, while sex, test order and body mass had no effect on performance (See Chapter 2: Table 2.1).

3.4.2 When did pheasants forage at feeders?

Pheasant foraging behaviour peaked at 60 minutes after civil dawn and decreased before peaking a second time between 2-3 hours before dusk (Figure 3.2).

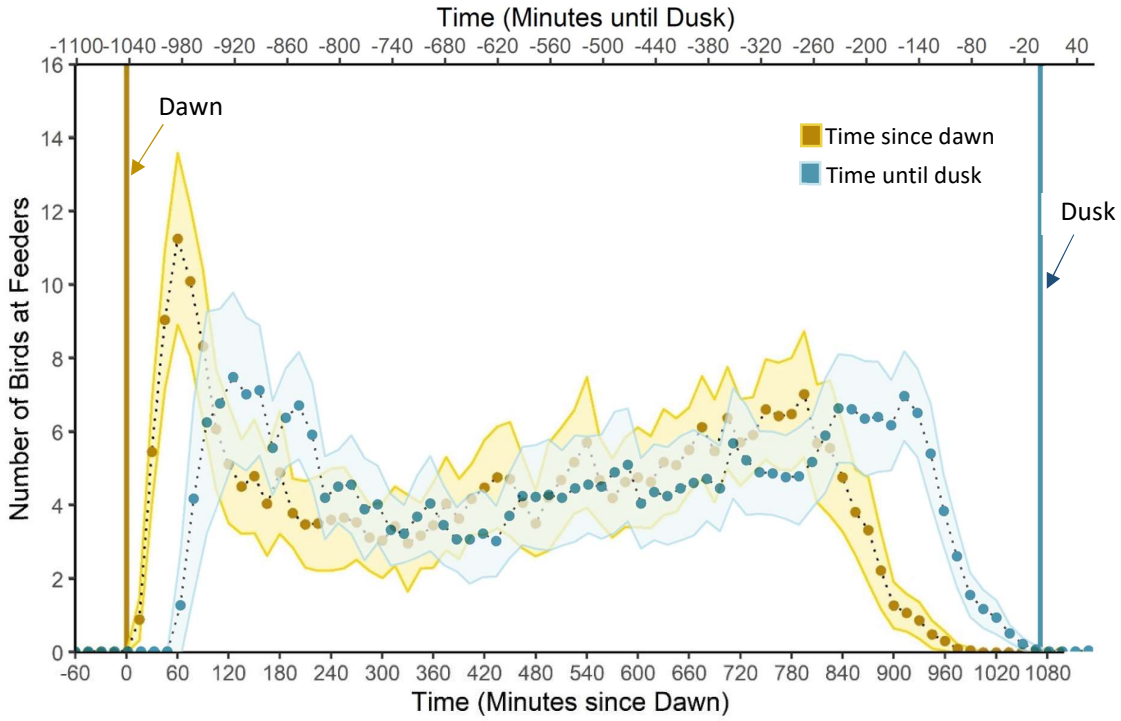


Figure 3.2 Foraging activity of pheasants for the number of birds present at any feeder per 15-minute interval since dawn – yellow bottom axis. Overlaid is the time until dusk – blue top axis, since the time difference between dawn and dusk varies with date. All data is from birds that were detected at feeders from 23rd July 2016 – 1st September 2016.

3.4.3 Are foraging onset times repeatable?

The median time of first arrival at a feeder per bird ranged from 76 – 651 minutes after dawn (mean of median time ± SD = 247.640 ± 109.547). A quarter of birds visited a feeder within the first hour post-dawn and half of the birds had visited a feeder within the first 3 hours post-dawn (Figure 3.3). An individual's time of first arrival had low but significant repeatablity (R=0.083 ± 0.014 [CI:0.057-0.112], n=173, p <0.001). The order of arrival at specific feeders by birds was also significantly (and more strongly) repeatable (R=0.144 ± 0.02 [CI:0.105-0.184], n=173, p<0.001). Since order of arrival was more repeatable, we only included this as our dependent variable in subsequent models, rather than testing both time and order.

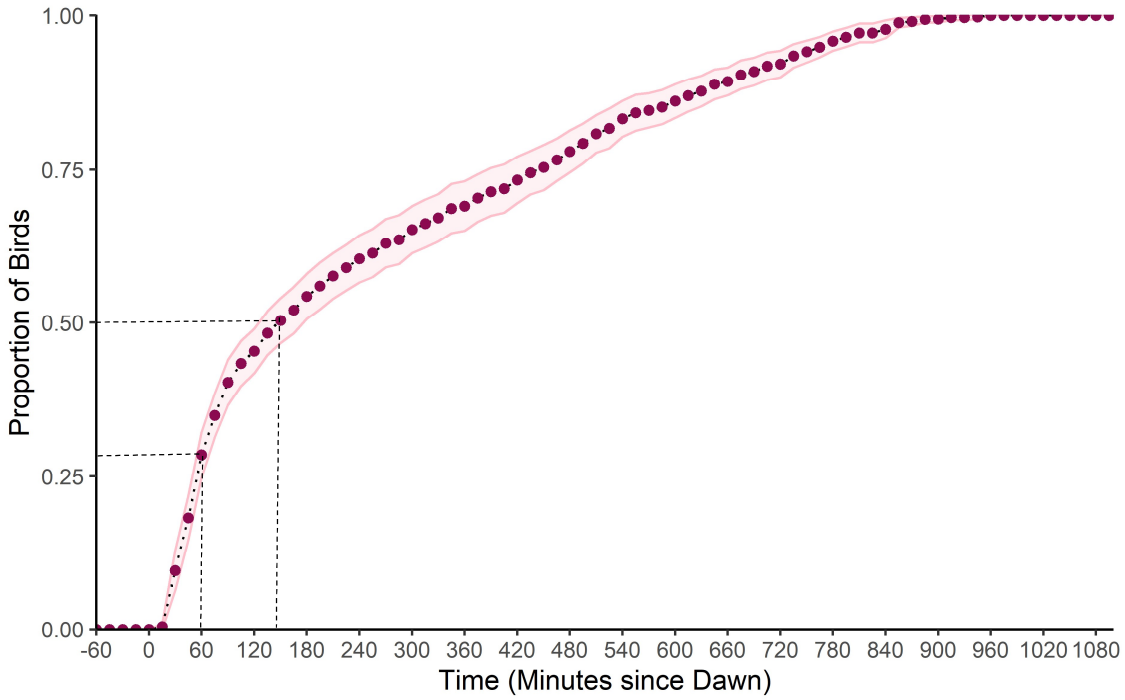


Figure 3.3 Cumulative proportion of birds' time of first detection at a feeder (RFID). Mean ± 95% confidence intervals. Sample size varies across days (min = 42, mean ± SD = 80.17 ± 34.468, max = 165) but all data is taken from between 23rd July and 31st August 2016

3.4.4 What factors influence the order of foraging onset?

Heavier birds arrived at feeders before lighter birds, but we found no evidence that spatial cognitive ability, sex or test order influenced order of arrival at feeders (Table 3.1). Furthermore, the relationship between mass and order of arrival was not influenced by sex, as demonstrated by a lack of interaction by sex and mass in the model. We conducted a post-hoc test (GLMM) to ask whether mass on release predicted the number of foraging bouts a bird had at feeders per day or the duration of foraging bouts to test whether arriving earlier increased total opportunities to forage. Mass was scaled using the *scale* function and we included sex in the model as males are often (but not always) heavier than females. Bird ID was included as a random factor and we included a Poisson error term with log link function. This post hoc analysis showed that heavier birds did not visit feeders more frequently than lighter birds (Estimate ± SE = -0.032 ± 0.036, LRT = 0.781, p = 0.377) nor did they visit for longer (Estimate ± SE = 0.031 ± 0.104, LRT = 0.090, p = 0.764). However, males visited feeders more frequently than females (Estimate ± SE = 0.220 ± 0.050, LRT = 18.28, p <0.001) and for longer (Estimate ± SE = 0.398 ± 0.142, LRT = 7.693, p = 0.006).

Table 3.1 Poisson GLMM results to predict order of foraging onset. Terms were dropped according to AIC and the order at which they were dropped from the full model is denoted in superscript by the parameter name. Parameters with an * are included in the final model.

Parameter	Estimate ± SE	LRT	n	P
Mass*	-0.073 ± 0.028	6.928	166	**0.008***
Cup Task[1]	0.018 ± 0.042	0.185	71	0.667
Median Test Order[2]	-0.001 ± 0.042	0.028	79	0.867
Top Bottom Task[3]	0.027 ± 0.039	0.472	79	0.492
Sex[4]	-0.046 ± 0.083	0.305	166	0.581
Sex x Mass[5]	-0.059 ± 0.083	0.0508	166	0.476

3.4.5 Did order of first forage influence survival?

Both sex and the order of arrival at feeders predicted survival chances. Pheasants that arrived at feeders later than others were less likely to survive than their earlier counterparts (Table 3.2). Males were also less likely to survive. Spatial cognitive ability had no effect on survival chances either as main effects or as an interaction with order of first arrival.

Table 3.2 Cox proportional hazard survival analysis. Terms were dropped according to AIC and the order at which they were dropped from the full model is denoted in superscript by the parameter name. Parameters with an * are included in the final model.

Parameter	Estimate	Hazard ratio [95%CI]	N (n events)	LRT	P
Median order of arrival (MOA)*	0.978	2.658 [1.862-3.795]	172 (36)	25.781	**<0.001***
Sex (Male)*	0.743	2.101 [1.060-4.166]	172 (36)	4.508	**0.034***
Mass[1]	-0.303	0.739 [0.263-2.079]	71(12)	0.325	0.569
MOA:Cup Task[2]	0.570	1.768 [0.445-7.017]	71 (12)	0.616	0.433
Cup Task[3]	-0.324	0.723 [0.327-1.600]	71 (12)	0.712	0.399
MOA:Top-Bottom Task[4]	-0.704	0.495 [0.148-1.650]	71 (12)	1.494	0.222
Top Bottom Task[5]	-0.457	0.633 [0.336-1.193]	71 (12)	2.012	0.156

3.5 Discussion

Pheasants showed individual-level consistency in both the time and the order in which they started foraging at feeders after having been released into the wild. Most birds began foraging at feeders within the first three hours post-dawn. Contrary to our predictions, spatial cognitive ability, as measured using both small and larger scale spatial tasks, did not predict arrival order at feeders. Instead, larger birds arrived at feeders before smaller conspecifics, regardless of sex and motivational traits. The order in which an individual started to forage had consequences for their survival, with birds that arrived at feeders later (and male birds generally) being the least likely to survive. Again, contrary to our predictions, we found no evidence that our measure of spatial cognitive ability was an important contributor to an individual's probability of survival.

We found low but significant repeatability in both time (R = 0.083) and order of arrival (R = 0.144) at feeders. This relatively low consistency in temporal foraging behaviour matches similar repeatability values for more broad scale (hourly) foraging activity in great tits (R = 0.14; Moiron et al., 2018). The remaining variance could be attributed to abiotic factors such as light intensity (Stuber et al., 2015), weather (Ferretti, Lovari, & Stephens, 2018) or temperature (Camp, Shipley, Milling, Rachlow, & Forbey, 2018). Daily differences in hunger levels, perhaps attributed to foraging efficiency in the day prior, may also contribute to this variance (Morgan, 1988; Whitham & Mathis, 2000). Furthermore, perceived predator threat (Brown, 1999) is also likely to be important for pheasants, since released pheasants suffer from high predation pressure (Madden, Hall, et al., 2018; Robertson, 1988) and this may differ between individuals depending on

their location. Finally, the density of birds at specific feeders may vary between locations and birds at 'busy' feeders are likely to fluctuate, at least in order of arrival since many individuals may be attempting to attain food simultaneously. Alternatively, the low repeatability of foraging onset time and order may be caused by differences in foraging tactics (Milligan et al., 2017), where birds that forage throughout multiple short foraging bouts might be more flexible with their foraging onset than birds that forage for long periods a few times within the day. Repeatability in similar traits such as onset of rest and awakening times has been suggested to be indicative of particular chronotypes in fish (Alós et al., 2017). This could also be the case for foraging behaviour. Such behavioural stability, if heritable, would provide a suitable basis on which selection could act.

Individual differences in rank order of foraging onset were best explained by an individual's mass. Specifically, the body mass of individuals on the day of release predicted the order of arrival at foraging sites whereby larger birds began foraging earlier than smaller birds. This was independent of sex, despite males being generally heavier than females (Whiteside, van Horik, et al., 2018) suggesting that in previous work demonstrating population level differences in foraging times between the sexes (where mass was not taken into account) (Whiteside et al., 2019), may have been driven primarily by individual differences in mass. Food motivation, as determined by test order during cognitive testing, also had no effect on the rank order of foraging onset. This may be due to large differences between the two environments (testing chamber and natural environment) in complexity, predation risk and interference from conspecifics which may mediate the 'motivation' in each context. Differences in absolute metabolic requirements increase proportionally with body size (Kendeigh, 1970; Peters, 1983) and

beginning foraging earlier would allow individuals a wider time period within which to consume their own nutritional requirements before dusk. However, we found no evidence to support this hypothesis as a post-hoc analysis showed that mass did not predict the frequency of foraging bouts, nor did mass predict the duration of foraging bouts.

Body mass has previously been shown to be an important ecological attribute that can influence a range of behaviours and interactions both within and across species (Peters, 1983; Woodward et al., 2005). For instance, competitive ability is commonly attributed to body size, where dominant individuals are frequently found to be larger than subordinates, giving them priority access to feeding sites (e.g Carrion crows, *Corvus corone* Richner 1989). During our monitoring period (21st July 2016– 1st March 2017), we did not expect competition to be high between pheasants, as feeders were large enough to accommodate multiple birds simultaneously. However, the high density of birds in the early stages of release could have encouraged competitive interactions. While we found that most individuals were present at feeders within the first 3 hours post-dawn, some individuals took almost until dusk (~900 minutes post-dawn) to visit a feeder. Pheasants are omnivorous (Hill & Robertson, 1988) therefore individuals that arrived at feeders later may have simply chosen to forage on other types of food. However, released pheasants are highly reliant on supplementary feeding (Draycott, Parish, Woodburn, & Carroll, 2002; Draycott et al., 2005; Whiteside et al., 2015) and therefore this is perhaps a less probable explanation than for other species. The steady increase of cumulative first visits throughout the day suggests that pheasants were attending feeders as their primary food source and

may have been excluded from feeders by larger individuals early on (as in great tits, *Parus major* Alatalo & Moreno, 1987).

Individual performance scores on two spatial cognition tasks were unrelated to the order at which birds arrived at fixed-site feeders. This is contrary to our prediction and one possible explanation for this is that routes to feeders are simple to learn, requiring only minor cognitive abilities to optimise. A second explanation is that birds may roost close to preferred feeding sites and this would reduce their navigational loads and risks of transit when they start foraging in the morning. It may therefore be necessary to also monitor roosting sites in future work. Similarly, differences in the size and structure of home ranges between individuals could have influenced the time at which individuals could arrive at feeders and it is possible that larger individuals could monopolise home ranges with easiest or quickest access to feeders (Alatalo & Moreno, 1987; Ofstad et al., 2016). A final explanation is that social factors could play an important role in determining the arrival of birds at feeders, overriding differences in individual spatial cognitive ability. Pheasants are gregarious and have been demonstrated to associate more strongly with birds of differing cognitive performance at foraging sites (Langley, van Horik, et al., 2020). It is plausible therefore that birds may follow ‘smarter’ individuals to a feeder and that a group of individuals with varied performances could arrive at feeders at the same time. In this case, social interactions, rather than individual cognitive ability, may shape temporal patterns of foraging.

Contrary to our expectations, we found mortality risk was not affected by an interaction between spatial cognitive ability and order of foraging onset which could have been indicative of remembering 'safer' routes to feeders; nor was mortality risk influenced by spatial cognitive ability alone. This latter result is particularly surprising as survival has been previously linked to spatial cognitive ability, tested using an open maze task, in multiple species (African Striped Mice, *Rhabdomys pumilio,* Maille & Schradin, 2016; mountain chickadees *Poecile gambeli* Sonnenberg et al., 2019), including pheasants (although indirectly and tested on a radial arm maze) (Whiteside, Sage, et al., 2016). These studies used tasks most similar to our cup task and therefore we would expect the cup task would be the most likely task to support our hypothesis. However, as mentioned in Chapter 2, it may also be that survival could be linked to a highly specific cognitive trait that we did not capture in our tasks or that we may not have conducted enough trials to accurately assess spatial cognitive ability with this task.

An individual's pattern of foraging onset was linked to mortality risk. Pheasants that arrived later at feeders each day were less likely to survive over the following seven months. This was a surprising result because pheasant mortality in the UK is commonly attributable to predation by foxes (Madden, Hall, et al., 2018). Foxes are crepuscular (Caravaggi et al., 2018) and so we expected them to be active and hence most threatening at dawn and dusk. Therefore, we expected pheasants arriving closer to dawn would have been more exposed to such predation risk and hence survive less well. One explanation for the pattern of mortality that we detected is that birds that consistently started foraging later had less time to assimilate food. Having lower food reserves could lead to starvation

directly but could also make individuals more susceptible to predation by making them more likely to take risks or were weakening them, reducing their escape propensity. A second explanation is that birds arriving later at feeders were surrounded by fewer conspecifics. While this may have afforded them greater opportunities to access the food, it might also have reduced the protection that collective vigilance can provide (Olson, Haley, Dyer, & Adami, 2015). Vigilance is likely to be mutually exclusive to foraging in pheasants (Whiteside, Langley, & Madden, 2016) so late arriving individuals, who are potentially in smaller group sizes or alone, are likely to either reduce their food intake or face increased risk of predation, both of which increase their risk of mortality. Mortality risk was also higher for males. This matches previous findings that male survival of released pheasants is lower than females (Madden, Langley, et al., 2018; Robertson, 1988), perhaps because males have a more conspicuous plumage or territorial behaviour, or their larger body size means that they have to forage more and hence are exposed to predators.

Selection has previously been suggested to act upon chronotypes (Alós et al., 2017; Martorell-Barceló, Campos-Candela, & Alós, 2018; Stuber et al., 2014). We show that fine-scale temporal foraging decisions are repeatable within free-roaming individuals and that the order at which pheasants attend artificial foraging sites is related to their survival probability. These individual differences in foraging onset were not explained by an individuals' spatial ability, suggesting that their timing of foraging is not governed by an ability to navigate more rapidly, or move effectively in low light. Surprisingly, individuals that start foraging earlier in the day, when we expected them to be more likely to encounter predators, were more

likely to survive. Therefore, selection may act on stable foraging onset times, but this is not influenced by cognition.

4 Coverage, accuracy and precision of a novel Reverse-GPS animal tracking system in a hilly and heterogenous environment

4.1 Abstract

Advances in tracking technology have revolutionised movement ecology but low cost, lightweight tags and high temporal and spatial resolution outputs are seemingly mutually exclusive factors when selecting a tracking system. We assess the relatively novel regional scale tracking system, ATLAS, which offers a solution. ATLAS uses programmable VHF tags (~0.7g without battery) and an array of receiver stations to detect the time of arrival for radio signals emitted from the tags, before collating the data in real time and sending detections to a central server. One key advantage of ATLAS is that data can be extracted from the server at any time, without the need to recapture individuals, from anywhere in the world. However, little has been done to assess the efficacy of the system in different environments. We monitored the coverage, accuracy and precision of a 4-receiver ATLAS system in the hilly farmland of North Devon, UK, an environment that does not necessarily lend itself well to radiotracking studies. We found that location was estimated more accurately when more receiver stations detected the tag, when the tag was within the perimeter of all detecting receiver stations and that the system was effective in woodland. Our site of interest had a median error of 46 m when compared to GPS, although it must be noted that our GPS unit itself was subject to error (~ 10 m in open landscapes), therefore our study may have underestimated the system's accuracy. Experiments assessing the accuracy and precision of stationary ATLAS tags in known locations revealed that the subsequent filters (a variance threshold based on signal-noise-ratio; median filter (5-minute fixed window) and a speed filter) created more accurate and more precise localisations. We found that the system provides sufficient coverage and accuracy to be utilised by a terrestrial, slow moving animal and provides numerous benefits including low cost and lightweight tags as well as

real-time tracking and data retrieval options that eliminate the need to retrap and retag subjects.

4.2 Introduction

Recent advances in technology have revolutionised wildlife tracking and allowed researchers to attain key insights into the cryptic movements of animals (Cooke et al., 2004; Rutz & Hays, 2009). To be useful, such a tracking system should record an individual's location with high spatial and temporal precision and accuracy at a sufficiently high rate and geographical coverage to capture the relevant intricacies of the individual's movement path over a long enough period of time to accurately represent movement patterns. This data should be reliably accessible to researchers deploying the system so that all tracked animals can provide information. The apparatus placed on the animal should also be light/compact enough to have no effect on the movement, more general behaviour or survival of the tracked individuals. Finally, the system should be affordable so that multiple individuals can be followed to ensure a representative sample. These four demands are in tension with one another: long-lasting tags with high sampling rates require large power sources; highly accurate systems are usually expensive; transmitting data from the tracked individual adds weight and technology costs to a system. Consequently, several different tracking systems are used with each representing a compromise over these four requirements.

Satellite-based systems such as ARGOS or GPS allow researchers to detect movements of animals across a global scale, aiding in the previously difficult study of marine species (Mate, Nieukirk, & Kraus, 1997) or of large scale migrations (Gill et al., 2009). However, the cost and size of tracking devices (hereafter tags) that report to satellites can often be prohibitive: cost can limit the

number of individuals that can be monitored simultaneously (Forbey et al., 2017); size, especially battery weight, limits their use to larger species. One simplification is that the tag does not transmit data but instead stores it until it can be retrieved. However, this can increase battery drain for GPS tags since they process and store data on-board. This technique also requires that the individual be relocated so that the tag can be retrieved, or data downloaded, increasing the risk that all data may be lost. The weight of tags, primarily comprising their battery, is critical and in order to avoid disrupting natural behaviour or mortality risk it is recommended to be no more than 2-5% of an animal's body mass (Kenward, 2001). This value varies across species according to their biology and ecology, and to avoid tag effects researchers should consider the mobility requirements of the animal, the species and the life stage of the animal of interest (Jepsen, Schreck, Clements, & Thorstad, 2005). While GPS tags have continued to be miniaturised in the last decade (10 g in 2007), the smallest GPS available in 2019 is still ~ 5 g (e.g. https://www.telemetrysolutions.com/). For many bird species, this is still too large. Out of 8734 bird species (Dunning, 2007), where mean body mass data is available (and is in some instances split between sexes: Combined = 2463, Female = 2391, Male = 2589, Unknown = 2296), only 37% of birds may be able to carry a nano-GPS (body mass > 100 g). While this is an increase from 2007 (19% of bird species, Wikelski et al., 2007), there is still a large deficit in the number of birds (and other small species) that can be tracked using this technology. Furthermore, GPS telemetry units for small animals can cost in the range of hundreds (sometimes thousands) of dollars each.

Radio-telemetry is the oldest remote-tracking technique (LeMunyan, White, Nyberg, & Christian, 1959) and is still a popular method for studying the

movement of species, ranging from insects (Drag & Cizek, 2018) to large carnivores (Seryodkin, Miquelle, Goodrich, Kostyria, & Petrunenko, 2017). Radio-telemetry tags transmit very high frequency (VHF) radio signals at set intervals which are detected by (generally) hand-held receivers (Kenward, 1987). Tags are light (< 0.2 g) (Kays et al., 2011) as they do not require large batteries since there is no on-board processing of data. Furthermore, radio-telemetry does not require the recapture of the animal to collect the tag and/or data (although see: Bouten, Baaij, Shamoun-Baranes, & Camphuysen, 2013). However, traditional radio-telemetry requires many hours of human interaction with hand-held receiver equipment, which limits the amount of location data that can be collected for multiple individuals simultaneously. Over half a century ago, attempts were made to automate this process and develop automatic, remote animal tracking systems using radio signals (Cochran, Warner, Tester, & Kuechle, 1965). However, until as recently as 2011 (Kays et al., 2011), the promise of these systems had still not been realised. The development of a system with temporal and spatial resolution rivalling GPS, but with the lightweight and long-life tags of radio-telemetry could revolutionise wildlife tracking.

Reverse-GPS systems, which use the time of arrival of radio signals transmitted by a tag to multiple stationary receivers, have proven to be a promising alternative to satellite and VHF systems (Maccurdy et al., 2009). These Reverse-GPS systems work on a regional scale (tens of kilometres) and require an array of clock-synchronised receiver stations at known locations to detect transmissions from radio (or acoustic) signals at unknown locations (Toledo, Kishon, Orchan, Shohat, & Nathan, 2016). This makes the system suitable for tracking non-migratory, residential individuals. One recent implementation of this system,

ATLAS, has been reported to provide similar accuracy to GPS (within tens of metres) (Weiser et al., 2016). The ATLAS wildlife tracking system was developed from the pioneering reverse-GPS system of MacCurdy et al. (2009), and improves on the original design by utilising beacons for clock synchronisation and enabling the quantification of uncertainty from the Signal to Noise Ratio (Weiser et al., 2016). Its lightweight radio transmitter tags cost less than $20 each and weigh under 2 g (Toledo et al., 2014), allowing more individuals and/or smaller species to be tracked while minimising the impact that tags could have on the behaviour of the subjects (Withey, Bloxton, & Marzluff, 2001). Furthermore, tags are programmable by the operator, allowing for study-dependant modifications to be made such as setting tag ID and transmission rates. This allows the frequency at which tags emit a radio signal to be reduced to improve battery life or increased to provide higher resolution location data. Tag-emitted signals are detected by fixed receiver stations, which consist of an antenna connected to a radio and a desktop computer and are synchronised using transmissions from beacons (tags at fixed known locations). Each receiver station calculates the estimated time of arrival of the signal and sends these to a central server via an internet connection (Fig. 4.1). If three or more receiver stations have detected the same signal, the server attempts to calculates the location of the tag using a multi-lateration algorithm and stores both detections and localisations in an SQL database. Users can then access the database to retrieve the location data for their study system. Users can also visualise an individual's location and movement in real time through the integrated desktop application, *Kamadata*, which aids in general monitoring of system health, as well as spotting the cessation of tag movement so that field researchers can investigate whether the tag has fallen off the animal or if the animal is dead. Both the system and within-range tags can be monitored

remotely from anywhere in the world if the database is set up to be accessible online.

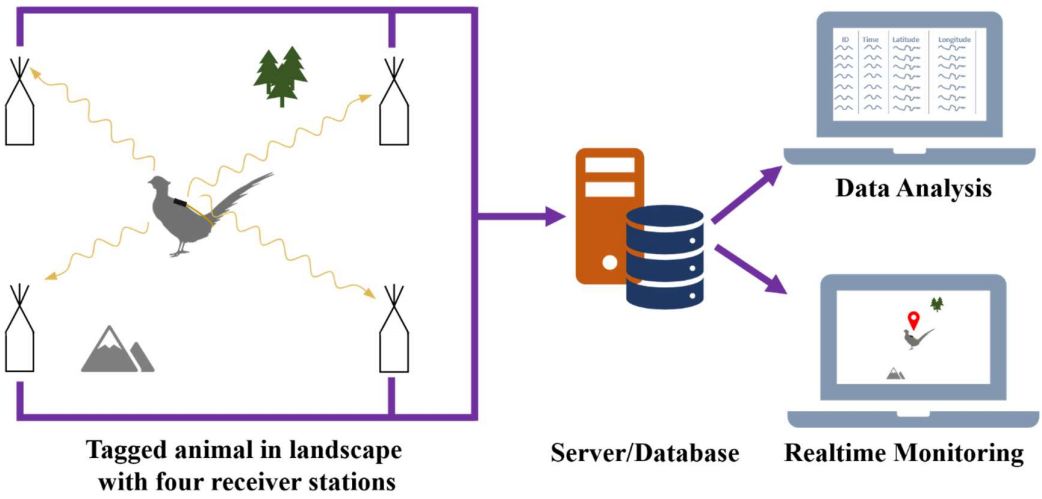


Figure 4.1 Schematic of ATLAS processing. An animal-mounted transmitter emits a signal which is detected by local receiver stations. These stations log the time of arrival of the signal and send this information to a server through an internet connection. Locations are calculated and stored on an SQL database which can be accessed remotely to extract data for data analysis or by the app Kamadata to visualise the system in real-time.

Studies using reverse-GPS are in their infancy and consequently, the efficacy and accuracy of reverse-GPS has not yet been fully assessed, especially in different landscape types. The original ATLAS system was established in the Hula valley in Northern Israel in 2014 and has since been used to monitor the movements of multiple species (e.g. Egyptian fruit bats, *Rousettus aegyptiacus* (Toledo et al., 2018), barn owls, *Tyto alba* (Weiser et al., 2016), Common Kestrel, *Falco tinnunculus*; Spur winded Plover, *Vanellus spinosus;* Coypu, *Myocastor coypus* (Toledo et al., 2014)). In the Israeli system, raw, non-filtered location data was recorded with a standard deviation of 5 m (Weiser et al., 2016), comparable to that of filtered GPS-derived locations. Receiver stations were located at the upper valley with clear line-of-sight of tagged animals located in the lower valley.

The lower valley itself is a flat, rural environment with little disturbance in the way of buildings, forests or hills. This provides optimal conditions for the introduction of a reverse-GPS system.

In addition to the original system, two other study sites have been established, each with their own unique challenges. First, receiver stations have been deployed in the Wadden Sea, Netherlands to assess foraging activity in a variety of shorebirds such as red knots (*Calidris canutus*) and sanderlings (*Calidris alba*) (A. Bijleveld, *personal communication,* 2019). The coastal landscape provides good line-of-sight opportunities for the transmission of radio signals and the researchers report that accuracy seems to be highest in the centre of their receiver array and decreases near the edges, although this has not been formally tested. Furthermore, the researchers have anecdotally reported that accuracy increases in areas covered by more receivers. This instigates a trade-off between coverage and accuracy which requires careful consideration for the ecology of the study system. Since shorebirds regularly travel large distances as the tides change, researchers at the Wadden sea ATLAS system opted to maximise the study area rather than increase the density of receiver stations and their system is reported to cover 600 km^2. Initial challenges included protecting the computer hardware from saltwater and the persistence of storms. A third deployment of the ATLAS system has been established in Potsdam, Germany which comprises 5 receiver stations at a University campus. They found some variation in the locations but have not formally quantified this (J. Pufelski, *personal communication,* 2018). Variation in their system could potentially be due to reflections of signals from buildings or interference from technical equipment within the university.

Despite the existence of several working ATLAS systems, none have yet conducted a formal assessment of accuracy (the distance from the true location), precision (the variance between locations) (Fig. 4.2) and/or coverage. The system, based on time of arrival of radio signals, is likely to suffer from considerable noise. Radio signals may be blocked or reflected by landscape features (Kenward, 2001). The precision and accuracy of a multi-lateration procedure is improved by increased numbers of receiving stations (or transmitters if GPS e.g. Hazel, 2009) and therefore tags that are only detected by a few receiver stations are likely to be less well localised. Finally, calculating localisations is most efficient when the tracked source lies within the perimeter of the receiver stations (the service area) (Cook, Buckberry, Scowcroft, Mitchell, & Allen, 2005). In the real world, all these conditions are likely to be violated for some tags at some time (anecdotal evidence suggests that low numbers of receiver stations, tags being on the edges or outside the receiver array and reflective surfaces such as buildings, may all negatively influence the success of a system), so it is necessary to understand how noise introduced by these violations is best accounted for and reduced. This may involve removing outlier localisations, filtering for inaccurate localisations and/or smoothing movement paths, but a robust and standard method to refine and interpret data from ATLAS systems has not yet been established.

Movement data frequently requires some filtering and/or smoothing before it can be used. Approaches to data filtering can involve: 1) the removal of locations which have been calculated using few reference points and so are unreliable; 2) the removal of locations that occur well outside the normal distribution of other locations and which cannot be explained by sudden erratic movements by the

tracked animal (this may be indicated by dramatic changes in speed or distance travelled by the tracked individual); 3) the smoothing of movement paths to instil greater biological realism and reduce the effect of erratic movement. One particularly robust and simple method of removing outliers is to introduce a median filter (Lim, Ng, & Da, 2008; Montillet, Yu, & Oppermann, 2007; Oudman et al., 2018), which can filter outliers while preserving some level of complexity. While aggregating data to calculate averages inevitably reduces temporal resolution, filtering data should improve overall spatial accuracy. In landscapes where we might expect some reflection it is also useful to consider additional filters that may improve overall accuracy while subjects move between reflective structures.

Speed and turning angle filters have also been shown to eliminate clear outliers in telemetry studies (Bjørneraas, Van Moorter, Rolandsen, & Herfindal, 2010; Christin, St-Laurent, & Berteaux, 2015; Patterson et al., 2010) and could be useful as an additional filter to catch signals that have been reflected far away for the duration of the median filter, although this likely depends on the duration of the median filter and the natural speed of the animal. For studies that use ARGOS (a satellite tracking system), Kalman filters (Kalman, 1960) have proved to be highly effective (Patterson et al., 2010; Sibert, Musyl, & Brill, 2003; Stoew, Jarlemark, Johansson, & Elgered, 2001), although these are sensitive to non-Gaussian errors and outliers (Wikle & Berliner, 2007). Filtering and smoothing data inevitably involves losing some resolution. Therefore, a trade-off occurs between having many unreliable raw data or few reliable data. Of course, the loss of data through averaging or filtering reduces the temporal resolution which may be critical to understanding animal movement, especially for rapidly moving

animals. Therefore, it is desirable to determine the most efficient filtering and smoothing methods that maximise accuracy and precision while retaining as much data as possible to ensure high temporal resolution.

We assessed the performance of the ATLAS system in rural Devon, South West England, which differs dramatically from each of the previous field sites in which ATLAS has been tested, in both topography and habitat. The landscape comprises of undulating terrain with small hills and valleys (ranging from approximately 140 m – 200 m above sea level) which may reflect radio signals or provide a barrier to system coverage. The habitat is largely farmland (improved grassland bordered by hedgerows) interspersed with blocks of woodland and small urban areas (mainly farm buildings), which again, could cause reflections of signals. The aim of this study was to assess the amount of reliable coverage that we can expect from our ATLAS system and to indicate its accuracy and precision in different areas of our field site. Furthermore, we aimed to establish and evaluate a simple filtering method to eliminate highly erroneous localisations and reduce overall location error in our data.

We present four analyses to investigate the efficacy of our system. First, we assessed ATLAS location error and system coverage as an experimenter moved around our field site on foot to mimic a tracked animal. The experimenter carried both ATLAS and GPS tags and we compared how well the localisations derived from the GPS and ATLAS units matched. ‘True’ positions were tracked using a GPS, although we acknowledge that GPS itself is likely inaccurate to some extent, especially near buildings or in woodland (Sigrist, Coppin, & Hermy, 1999),

therefore we also assessed the GPS error in different areas of our field site. Second, we monitored ATLAS location error and the reliability of receiver stations by placing tags for extended periods in fixed locations where the actual location was known and did not deviate. Thirdly, we assayed the efficacy of three sequential filters on the raw data from the stationary tags and investigated improvements in accuracy and precision. Finally, we provide an example of the application of these filters on track data collected from free-roaming pheasants, *Phasianus colchicus*.

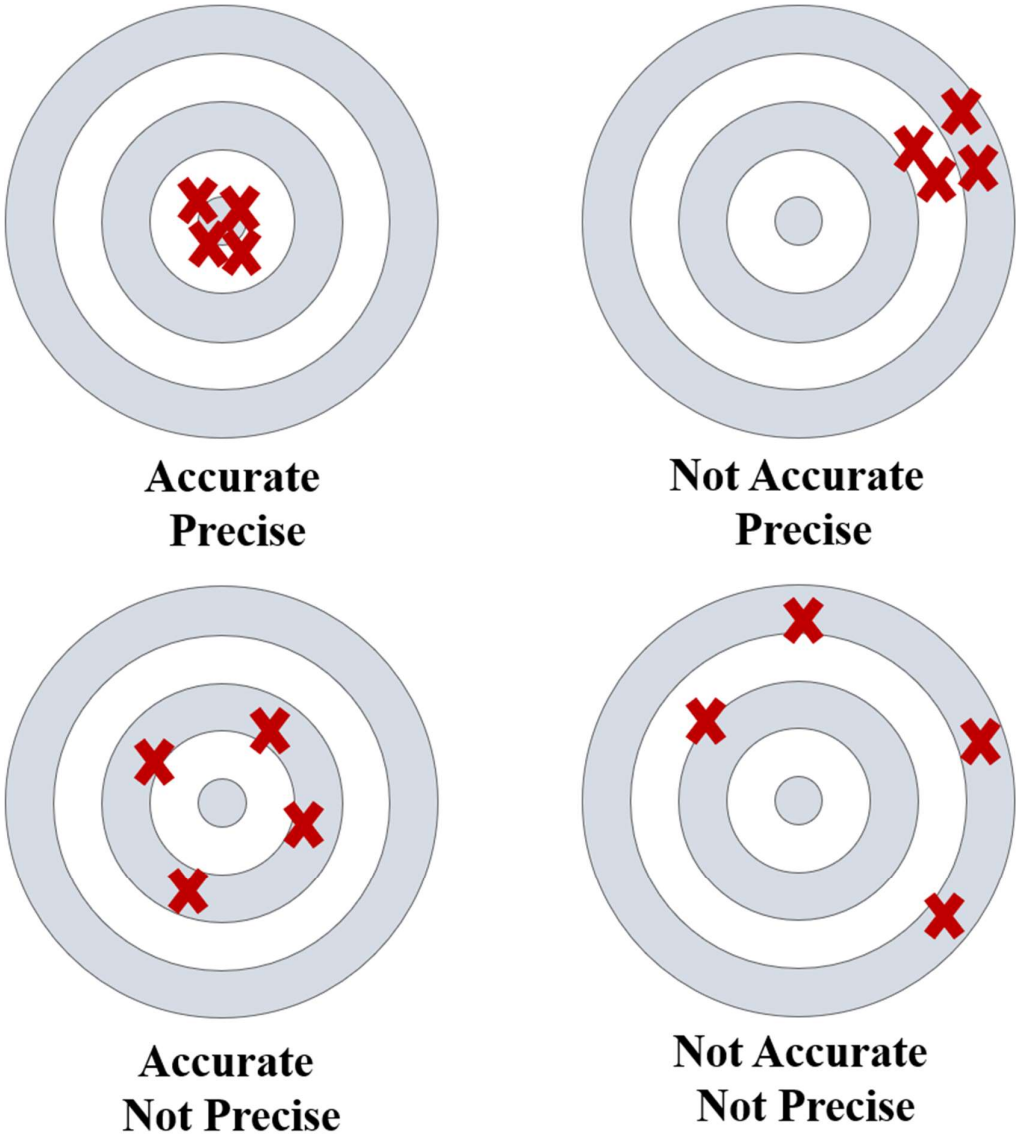


Figure 4.2. Infographic to define the differences between accuracy and precision.

4.3 Methods

4.3.1 ATLAS system

Receiver stations consisted of desktop computers (Windows 10, 2 GHz, 16 GB RAM, Intel i7 processor) connected to a USRP N200 radio unit with WBX-40 daughter board and GPS disciplined oscillator (GPSDO) (Ettus research). These were situated in buildings or in waterproof boxes with access to mains power. A GPS antenna (Ettus research) was connected to the GPSDO. A UHF antenna (Diamond X-30N, Martin Lynch & Sons Ltd, Middlesex) was connected to the radio through a custom-built front-end unit (CircuitHub) and a Masthead LNA (L434LNACN, Down East Microwave).

An array of four receiver stations were placed at the highest points in the landscape overlooking the centre of our study site, a pheasant release pen (latitude = 50.772022, longitude = -3.901460) (Fig. 4.3). These were situated on the roofs of buildings (N = 2) or on pylons/windmills (N = 2). Latitude, longitude and height above sea level for the base of each antennea were measured using a Trimble R6 GNSS receiver (precision = 1-2 cm; Korec, https://korecgroup.com/) and precision was calculated using Trimble's VRS now service, downloaded in the field via data sim. For receiver stations 1 and 3, we were unable to reach the antennae using the Trimble and therefore took a reading for height above sea level at ground level and used a laser (SW-T40, SNDWAY) to measure the height of the antenna above ground level to add to the total. Each desktop computer was connected to the internet using a 4G dongle (Huawei E3531, Genuine UK). Two beacon tags were placed at locations where SNR was low at all four receiver stations (Fig. 4.3).

Our server was also a desktop computer (Windows 10, 2 GHz, 16 GB RAM, Intel i7 processor) but was situated in the University of Exeter (Exeter, UK). The server collated and stored data in a MySQL (v5.7, https://www.mysql.com/) database.

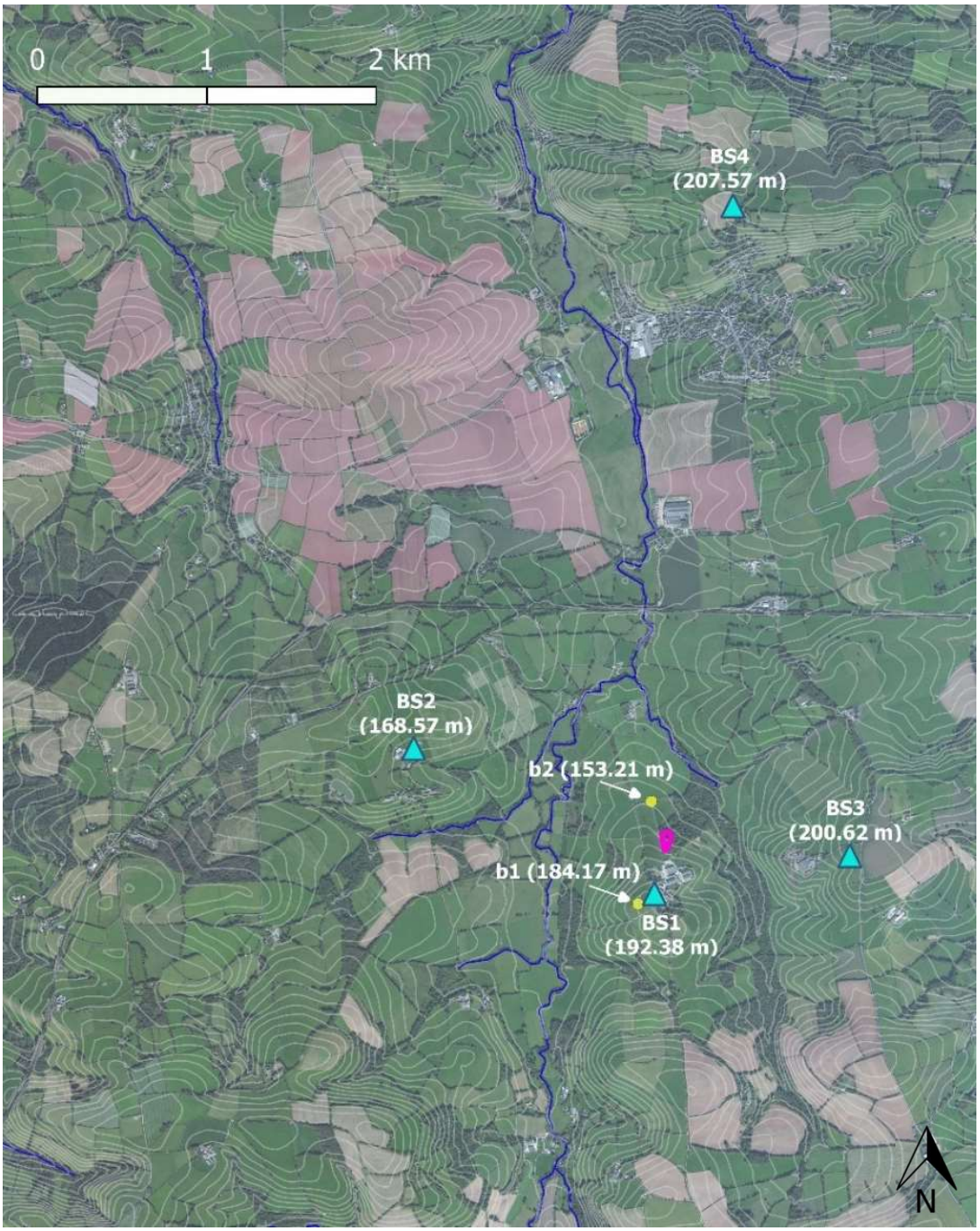


Figure 4.3. Landscape around the pheasant release location (pink outline) and locations of receiver stations (BS, blue triangles) and beacons (b, yellow circles) for the ATLAS system. Height above sea level for receiver stations and beacons is shown in parentheses. Bing aerial map provided the background with 5 m contours.

4.3.2 Tag Design

Miniature frequency-shift-keying transmitters and an MSP430 microcontroller were used to create the ATLAS tags (Fig. 4.4) with a multistrand (27 strand) stainless steel, gold-coated antenna (~15 cm long). Tags were powered by an AA sized Li-$SOCl_2$ battery (2.6 Ah 3.6V) with integral solder tags (SAFT) and which, once fully assembled, weighed 22 g (2-3% of pheasant body weight) which

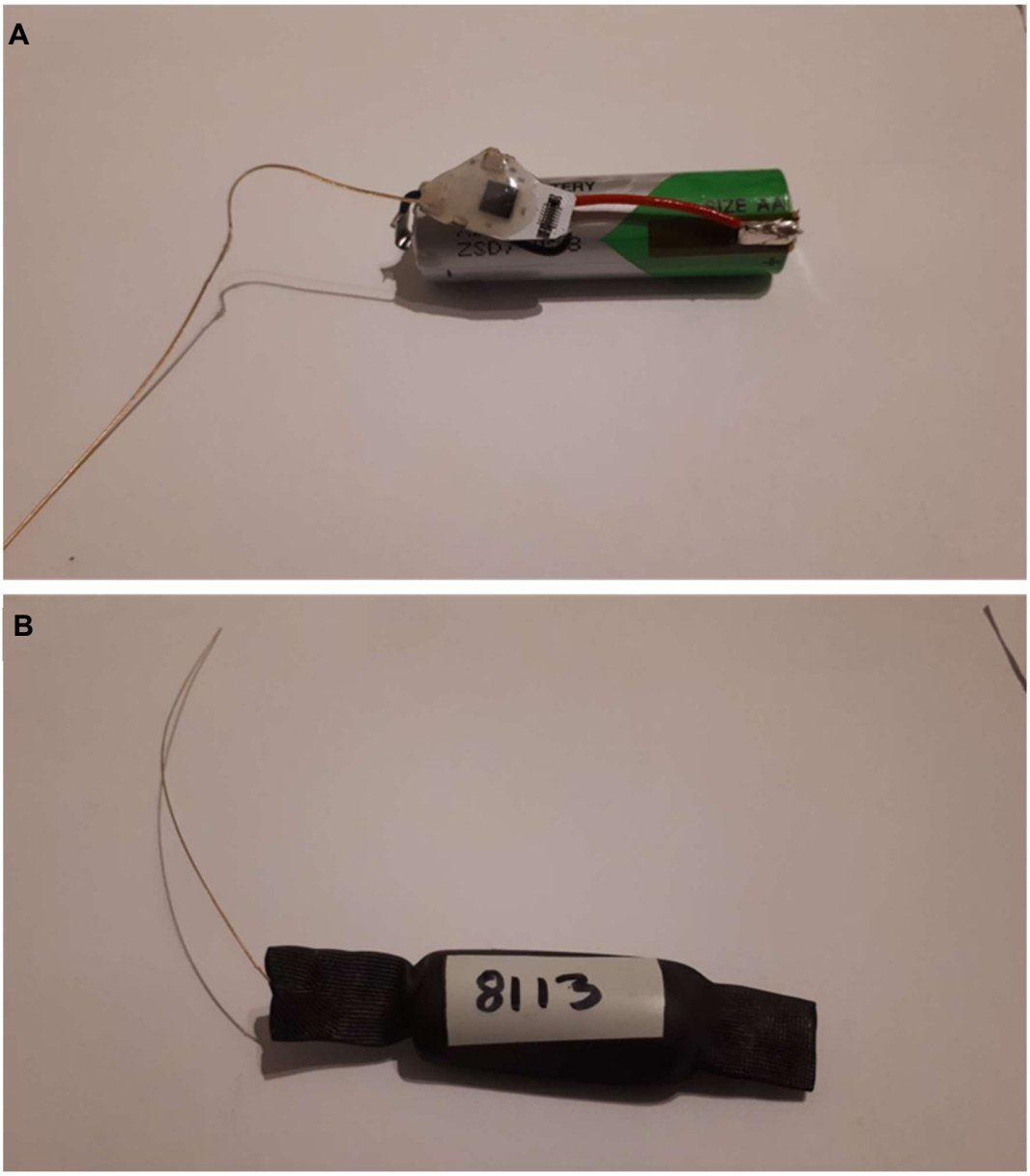


Figure 4.4 A) Programmed tags are covered in epoxy resin and attached to a battery (AA sized Li-SOCl2), before being B) enclosed in heat shrink.

is deemed to be an appropriate weight for a primarily terrestrial bird (Kenward, 2001). Tags were programmed to transmit 8192-bit codes at a frequency of 1 Hz (beacons) or ¼ Hz intervals, matching the frequencies that we used to track our pheasants. We set our pheasant tags to ¼ Hz as we aimed to extend battery life and since pheasants move relatively slowly, we did not feel that this would negatively impact our assessment of their movement. We therefore used ¼ Hz in all our testing. After programming, tag circuitry was protected using a coating of epoxy resin and then the battery and programmed chip were sealed in heat shrink tubing to further protect the tag from damage.

4.3.3 Moving tag experiment

Our first method of assessing accuracy and coverage of our ATLAS system was for an experimenter (CB) to walk around our field site (Fig. 4.5). The experimenter was equipped with a handheld GPS logger (set at 1 Hz) on an android smartphone ('*GPSLogger*' app), and an ATLAS tag (set at ¼ Hz) attached to their leg (~30 cm from the floor which is comparable to pheasant height). Over 5 sessions we collected 549 minutes of location data through both GPS and ATLAS. After assessing the accuracy of our GPS unit (see below), we used GPS positions as a reference to the 'true' location of the experimenter and ATLAS tag. We then assessed the current coverage of our system by calculating the fix rate (number of localisations/total number of possible localisations). We also report the number of receiver stations that detect each tag transmission (0-4) throughout the moving tag experiment to give an indication of potential coverage.

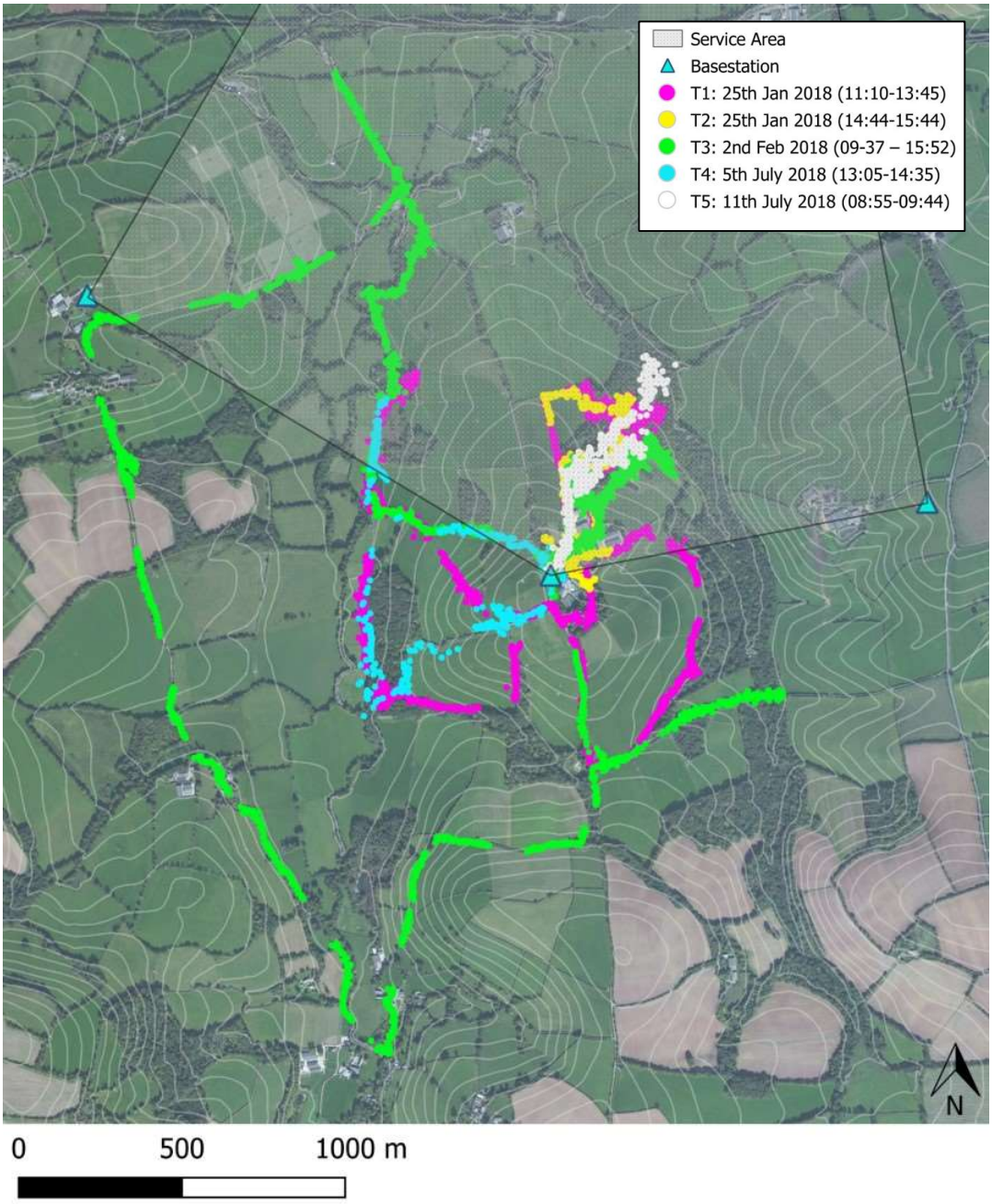


Figure 4.5 Plotted GPS localisations (points) showing the routes taken for the moving tag experiment. Clear gaps in the routes are where GPS did not give a localisation. Five trials took place and the date, time and route of each trial can be seen in the legend. Colour denotes trial. Receiver stations and their presumed interior service area is shown.

4.3.4 Assessing the performance our GPS unit

We acknowledge that some error from our GPS unit is unavoidable, therefore we attempted to assess the accuracy of our GPS unit relative to conspicuous landscape features as well as the reliability of the unit in producing localisations

across habitats and over time. This was necessary in order to provide a baseline against which we could compare the ATLAS tag performance (see below). We estimated the error of our GPS by eye, through plotting the GPS positions on a Bing satellite layer (print rights under the Microsoft ® BingTM Maps Platform API's Terms of Use, April 2019) in QGIS (QGIS Development Team, 2017). Where a clear path was present, i.e. on roads or tracks, we measured the distance perpendicular from our estimated 'true' location e.g. the road, to the nearest GPS point to obtain an estimate of GPS accuracy. We took 35 measurements at relatively regular intervals (~ 300 m) for locations where the path taken by the experimenter was obvious. However, we were only able to assess this accuracy in open landscapes with narrow roads, leaving few possible deviations from an obvious route. Some of our routes included wide farmyards (which we denote as 'urban' in this context due to the potential for signals to reflect off man-made structures) and woodland for which we were unable to identify a clear route from satellite images. Furthermore, GPS locations had a much higher spread of estimated locations around farm buildings and in woodland. We therefore did not obtain an estimate for GPS accuracy in urban and woodland environments and GPS accuracy measures from these areas should be interpreted with caution. We also calculated the reliability/coverage of our GPS unit by calculating the actual fix rate (total locations/total possible locations at 1Hz) for each trial.

4.3.5 Assessing the performance of a moving ATLAS tag

We assessed the coverage of the ATLAS system in two ways. First, we calculated the fix rate by dividing the total ATLAS locations by the total possible locations at ¼ Hz in the given time period of each trial. Second, we collated the detections of

the tag from each receiver station and counted the number of detections within 0.01 seconds of each other. We then matched the timestamps of these detections to the nearest temporal GPS location and calculated the dime difference (seconds) between the detections and the GPS localisation time. If there was no GPS location available within 4 seconds of an ATLAS detection (perhaps because GPS had failed to achieve a fix), then this ATLAS point was disregarded as we did not have a clear estimate of the 'true' location of the tag. Alternatively, if there were no ATLAS detections within 4 seconds of a GPS location, then the location was determined as having zero receiver stations able to detect the tag in that location. From this, we could say how many receiver stations detected the ATLAS tag while it was located at an approximate location, determined by the GPS.

We assessed the accuracy of raw ATLAS data by comparing distances in metres between the ATLAS-derived location and the closest temporal (within 1 second) GPS-derived location. First, we assessed the accuracy of the immediate vicinity (<450 m) of our release site, since for the first month post-release most movement is in this area. We then assessed the factors that may affect accuracy by categorised each GPS localisation from all moving tag trials into a habitat type: Woodland, Urban or Open (roads, tracks or fields). To do this, we added habitat attributes to the dataset by matching GPS localisations with a habitat layer created using QGIS (QGIS Development Team, 2017). We used the National Forest Inventory Woodland GB 2017 shapefile (accessed 21st February 2019: http://data.gov.uk) for woodlands (defined as a minimum area of 0.5 hectares with a minimum width of 20 m unless a narrow corridor connects two or more woodland areas). We added polygons manually over anthropogenic structures

such as farms and homes to classify ‘Urban’ habitat, using the Bing satellite layer as a guide. No other habitat types were large enough to be relevant on our field site, therefore the remainder of land was classified as ‘Open’. These included grazing ground, unimproved grassland, hedgerows and two small areas of wetland. We also created a polygon whose perimeter connected the 4 receiver stations (hereafter ‘service area’) and calculated whether the GPS location was on the interior or exterior of the service area perimeter. Our most southern receiver station was relatively close to our release pen (~300 m away) resulting in a high likelihood of pheasants moving into the exterior of the service area, therefore assessing the accuracy of both the interior and exterior of the service area is relevant for our subsequent study.

4.3.6 Stationary tag experiment

We placed 16 ATLAS tags in areas known locations for 30 minutes (Fig. 4.6). Seven of these were placed around the immediate vicinity of the field site, in places pheasants were likely to visit. Eight tags were placed in the surrounding landscape by the sides of roads (as we could not access the nearby woodland or fields). One tag (J on Fig. 4.6) was placed at a windmill that we were assessing for a 5th receiver station. Tags were placed in areas that we had safe and legal access to, either on foot or by car, but we were unable to place tags in a grid formation due to a lack of access to private fields or lack of footpaths on busy roads. We attempted to achieve a wide distribution of tags and for any areas that we missed in the moving experiment. We assessed how reliable, accurate and precise the ATLAS system was at identifying these tag locations in two ways.

First, we monitored the number of receiver stations that detected each tag within each localisation period (4 seconds) to assess coverage and receiver station reliability. We assessed the overall reliability of receiver station detection rates by measuring how many receiver stations detected each tag transmission (where at least one receiver station detected it). This gave us the number of tag transmissions detected by one, two, three or four receiver stations.

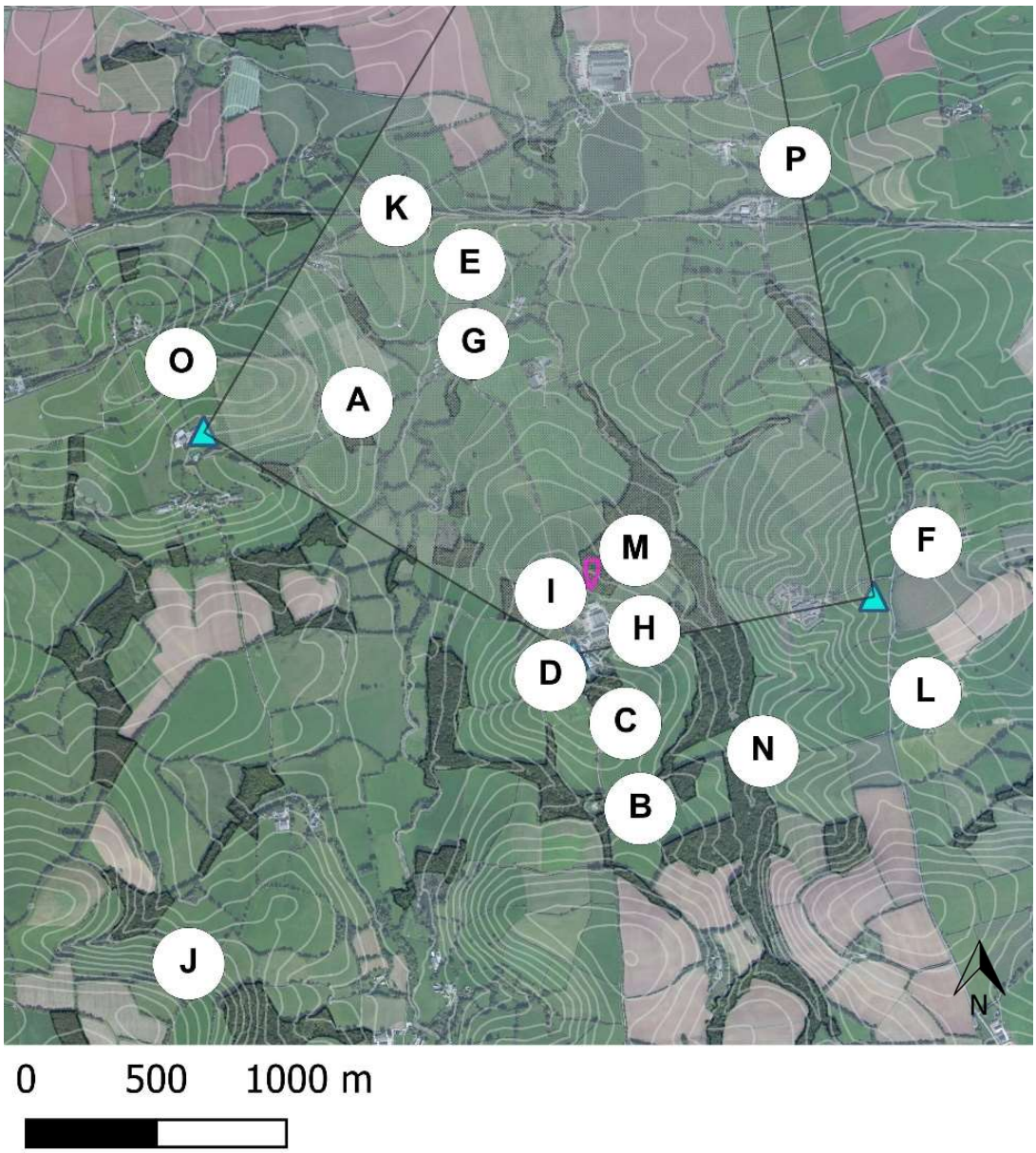


Figure 4.6. Locations of stationary tags. Reference for tags links to Table 3 in the results.

Second, we assessed accuracy by calculating the distance of each ATLAS estimated location from the 'true' location for each tag (determined by GPS) by calculating the maximum distance within the 50th and 95th percentile of localisations. We measured the precision of localisations by calculating the standard deviation of the error (distance from true location, determined by pinpointing the location on a Bing Satellite layer through QGIS (QGIS Development Team, 2017).

4.3.7 Assessing the performance of data filtering to improve localisation accuracy and precision

To eliminate inaccurate localisations and reduce location error, we applied multiple filters to the raw data provided by the ATLAS system on our moving and stationary tag experiments. We deployed our filters in sequence. First, we removed data points that were likely to be unreliable because they were detected with high variance. ATLAS produces a variance-covariance matrix as descriptors of variance when extracting localisations. We found that by simply applying a threshold value (we chose 75, see Fig. 4.7A) for the variance reported in the x and y axes (hereafter the VarXY filter) allowed us to remove highly erroneous localisations. Our second filter involved calculating the median value of x and y coordinates 5-minute fixed time windows, which reduces temporal resolution but has previously been found to be a robust and accurate method of filtering location data so that outliers are removed (Pastell, Frondelius, Järvinen, & Backman, 2018). We considered the ecology of the pheasant to choose an appropriate time window for our median filter.

Pheasants are relatively slow moving (Fig. 4.7B) and rarely fly, therefore we felt that a 5-minute time window would give us enough data to balance the reduction in temporal resolution with an increase in spatial accuracy. We expect ~75 localisations in 5 minutes at ¼ HZ. Any medians that were created with less than 5 data points were removed, since it was unlikely that outliers could be removed effectively with this amount of data. Our final step in the filtering protocol was to try to remove any large 'jumps' in location that were likely to be caused by interference or reflections rather than biological movement. Previous work suggests that erroneous spikes in location estimates can be removed by setting a maximum speed threshold and an angle threshold which should be based on the biology of the animal in question (Bjørneraas et al., 2010).

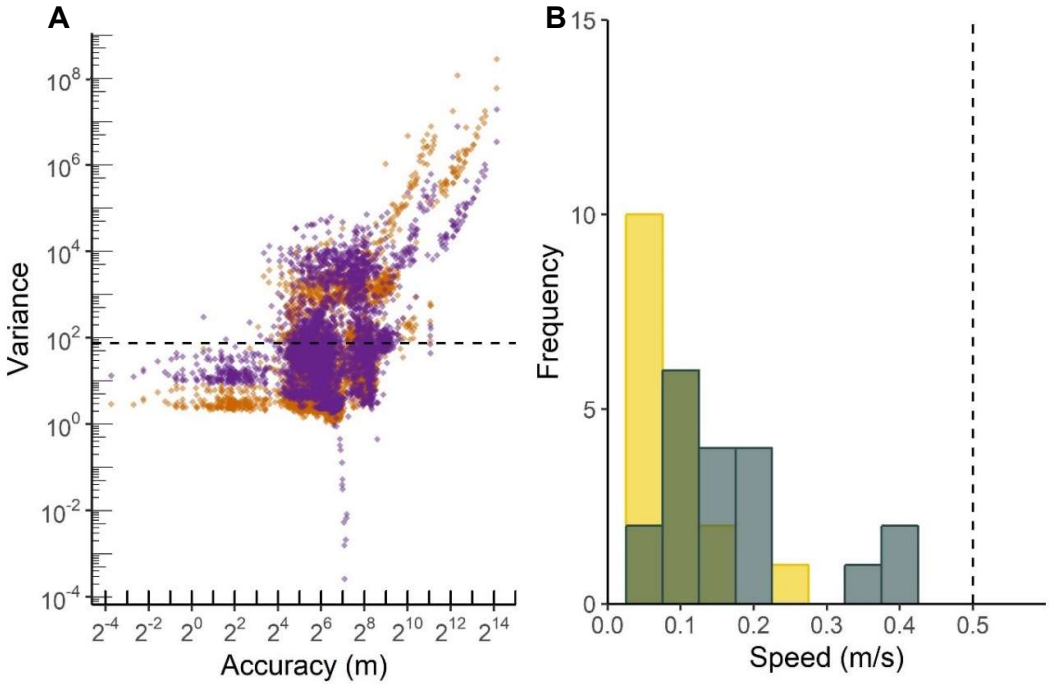


Figure 4.7 A) The effect of variance in the X (orange) and Y (purple) axes for atlas localisations on accuracy. The most accurate date falls below 75 (dotted line) which was therefore chosen as a threshold value. B) Median speed of free-roaming pheasants (95th percentile: yellow, 99th percentile: grey, dotted line = pheasant-specific cut off point). GPS tracks were collected at 1Hz but are summarised to 5-minute medians to make it comparable to the testing.

We investigated potential thresholds for speed and angle filters by assessing a sample of GPS tracks that we had collected from free-ranging pheasants. Between 16th March 2017 and 27th June 2017, we captured 19 adult pheasants (14 female, 6 male) in baited funnel traps and attached a combined GPS (IGOTU GT120) and radio tag "backpack" using water soluble wing straps. Depending on the time of year, the birds were either released immediately at the trap site (2 males, 8 females) if they were caught between March-May 2017, or at a woodland on the outskirts of our field site (latitude = 50.775516, longitude = -3.933363; 2 males, 5 females) in May-July 2017 to prevent competition with younger pheasants that were released in late July. The backpacks were released from the birds once the straps dissolved in water (e.g. during rainfall or by contact with dew in long grass). We then located the GPS and its attached radio-tag using a handheld radio tracking antenna (Field Marshall Digital Tracking Receiver FM

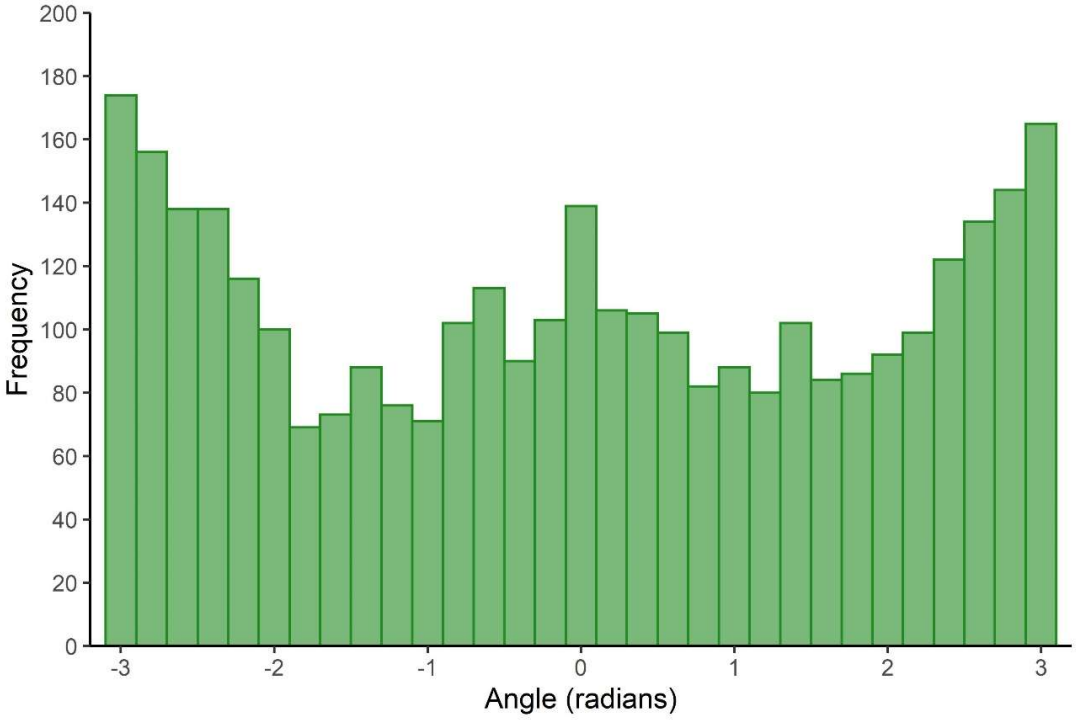


Figure 4.8 Turning angles (radians) for trajectories of free roaming pheasants tracked with GPS. GPS tracks were collected at 1Hz but are summarised to 5-minute medians to make it comparable to the testing.

UHF 2000 Marshall radio Telemetry, Cumbria, UK). The GPS units collected location data at a frequency of 1 Hz. GPS track durations had a mean ± SD of 27.371 ± 0.709 hours of daylight movement (the GPS units did not record location data between 10 pm and 5 am when pheasants were roosting). We calculated 5-minute medians of GPS localisations and calculated the speed and turning angle between each step. We then calculated the 95th and 99th percentile for each bird's speed to determine an ecologically realistic maximum speed for our study species (Fig. 4.7B). The maximum individual 99th percentile speed was 0.4 m/s therefore we determined that 0.5 m/s would be a realistic speed filter threshold for pheasants. We could not determine a clear angle threshold value for pheasants (Fig. 4.8). This may be because pheasants move very slowly therefore even small positional errors allow for the range of available turning angles to occur frequently. To retain as much data as possible, and because the slow movement speed of pheasants allows for a low speed threshold to be set, we determined that an angle filter would not be useful for our model species. The chosen sequence for filtering is shown in figure 4.9.

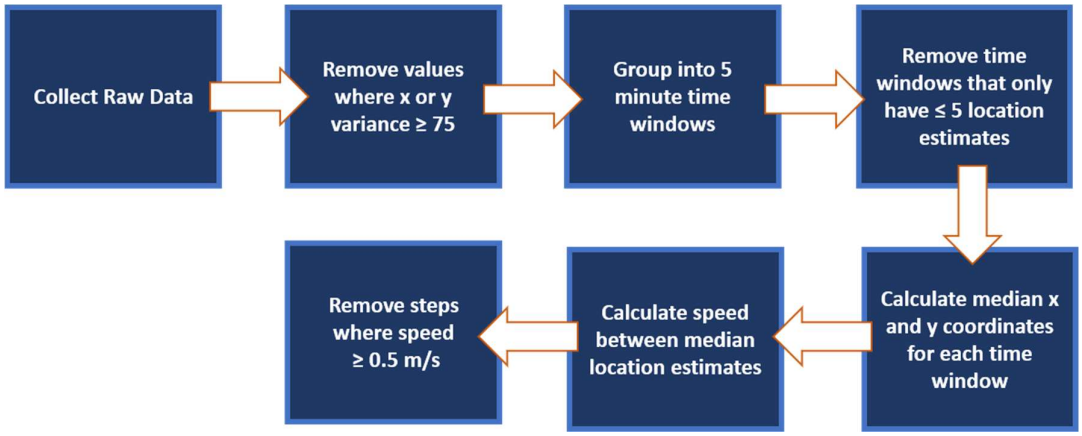


Figure 4.9 Sequence for filtering raw ATLAS data. Speed filters (step 7) should be specific to the study species.

4.3.8 Assessing the performance of the ATLAS system on free-ranging pheasants

We utilised real data from our study system (See appendix for details) from our 2017-2018 field season in two ways. First, we examined four, specific visual examples of how filters influence the precision of tracks over one day on a real bird. Second, we collated all our pheasant movement data onto one map to visually assess the coverage area of ATLAS on our field site when detecting moving released pheasants. We reared 184 pheasants in 4 replicated enclosures over a 10-week period for another experiment (see Chapter 5 for details). Briefly, the birds were habituated to humans from one day old and voluntarily took part in behavioural tasks to measure individual differences in their cognitive abilities. At 9 weeks old, we attached ATLAS tags (22 g) to juvenile pheasants (range: 700 - 1100 g). Elastic wing-straps were threaded through the ends of the heat shrunk tubing to create a harness. We checked whether the harnesses caused damage to the birds by leaving the tags on while they were still captive for one-week. We checked the underside of wings after day 1 and adjusted the lengths of the straps if they were deemed to have been ill-fitting. We checked the harnesses again on the day before release (day 6) and on the day of release. We did not find any injuries on birds due to wing straps. At 10 weeks old, the juvenile birds were released into an open-topped pen (latitude = 50.772968, longitude = -3.901693), surrounded by 6 ft fencing and a 1 ft high electric fence to deter predators. Birds could disperse from the enclosure at will by flying over the fence and could re-enter using one-way entrance holes. Birds were provided with supplementary food (wheat) distributed by 43 barrel-feeders throughout the surrounding area. Birds were then tracked by the ATLAS system from 27th July 2017 until 1st February 2018.

4.3.9 Statistical Analysis & Software

Data analysis was conducted using a combination of R (v3.5.3) (R Core Team, 2019) in RStudio (v1.2.1335) (RStudio Team, 2018) for statistical analysis and figures, and QGIS for map creation (v3.4) (QGIS Development Team, 2017). We calculated the median error and confidence intervals of the median using the *groupwiseMedian* function from the *rcompanion* package (v2.2.1) (Mangiafico, 2019). The *distm* function from the *geosphere* package (v1.5-7) (Hijams, 2017) was used to calculate distances between locations. To assess the difference in accuracy and precision produced by filters we conducted a paired samples Wilcoxon test in R between the 50^{th} and 95^{th} quantile of raw and filtered data and the standard deviation of raw and filtered data for each of the stationary tags. We used a general linear model (GLM) with a Gamma error structure and log link function to investigate whether habitat type (open, urban, woodland), number of receiver stations that detected the tag (3 or 4) or whether the tag was on the interior or exterior of the service area influenced the accuracy (distance between ATLAS localisation and GPS localisation) of the system.

4.4 Results

4.4.1 How accurate is our GPS unit?

For open areas where we could easily determine the route the experimenter took, the GPS had an estimated error of ~10 m (mean ± SD: 10.114 m ± 11.867, range 2-58 m). We could not calculate an accuracy estimate for Woodland or Urban areas because we could not trace the route of the experimenter post-hoc. Our GPS unit produced far fewer localisations than would be expected if it was perfectly reliable. At the 1 Hz setting we applied to the GPS unit, we would have expected 33055 localisations across all five walks, but we collected only 8641 (26.14%; Table 4.1).

4.4.2 Coverage and fix rates

4.4.2.1 Moving Tag Experiment

Detection of our tags by ATLAS was good, with almost continual coverage throughout our study site. We collated 8468 separate detection times (within 0.01 s of each other) for ATLAS transmission detections at all receiver stations. We found some minor discrepancies where a tag was detected by one receiver between 0.1-1 (n=243) second after other stations had recorded the transmission. Attempting to combine these with their closest detection times led to 5 receiver stations detecting a tag within a 4 second period, which was not possible, therefore we did not do this. This discrepancy is important to note as at ¼ Hz transmission rate, we would have expected ATLAS tag transmissions to have been detected a maximum of 8263 times over all 5 trials therefore some (at least 205 = 2.4%), but not all detections have been duplicated, however it is impossible to determine post hoc which are original detections and which are

replicates. Only 104 (1.2%) of these detections were recorded with a greater than 4 seconds difference from a GPS location, indicating that no receivers detected the tag at these locations (Table 4.1). Therefore, ATLAS detected transmissions at 98.77% of GPS locations. It is important to note that these are detections, rather than localisations.

Localisations of our tags by ATLAS, generating useable positional data was less consistent. 5750 tag transmissions were detected by 3 or more receiver stations, indicating that they were eligible to produce a localisation (Table 4.1). From these, we collected 5723 localisations (69.26% of expected localisations) from ATLAS indicating that 27 detections where ≥3 receiver stations were reached failed to generate a localisation. Areas where >3 receiver stations detected a tag were typically spatially clustered (Fig. 4.10)

Table 4.1 Number of receiver stations that detected each tag transmission over the five moving trials. Note slight discrepancy as total is 8648 and should be 8263

Number of Receiver stations	Zero	One	Two	Three	Four
Number of Tag Detections	104	763	1851	2626	3124

4.4.2.2 Stationary Tag Experiment

The number of receiver stations detecting a tag did not only vary in space across the study site, but also varied over time while the tag remained in a single location

We identified three locations that were only detected by one or two receiver stations and therefore could not produce any locations.

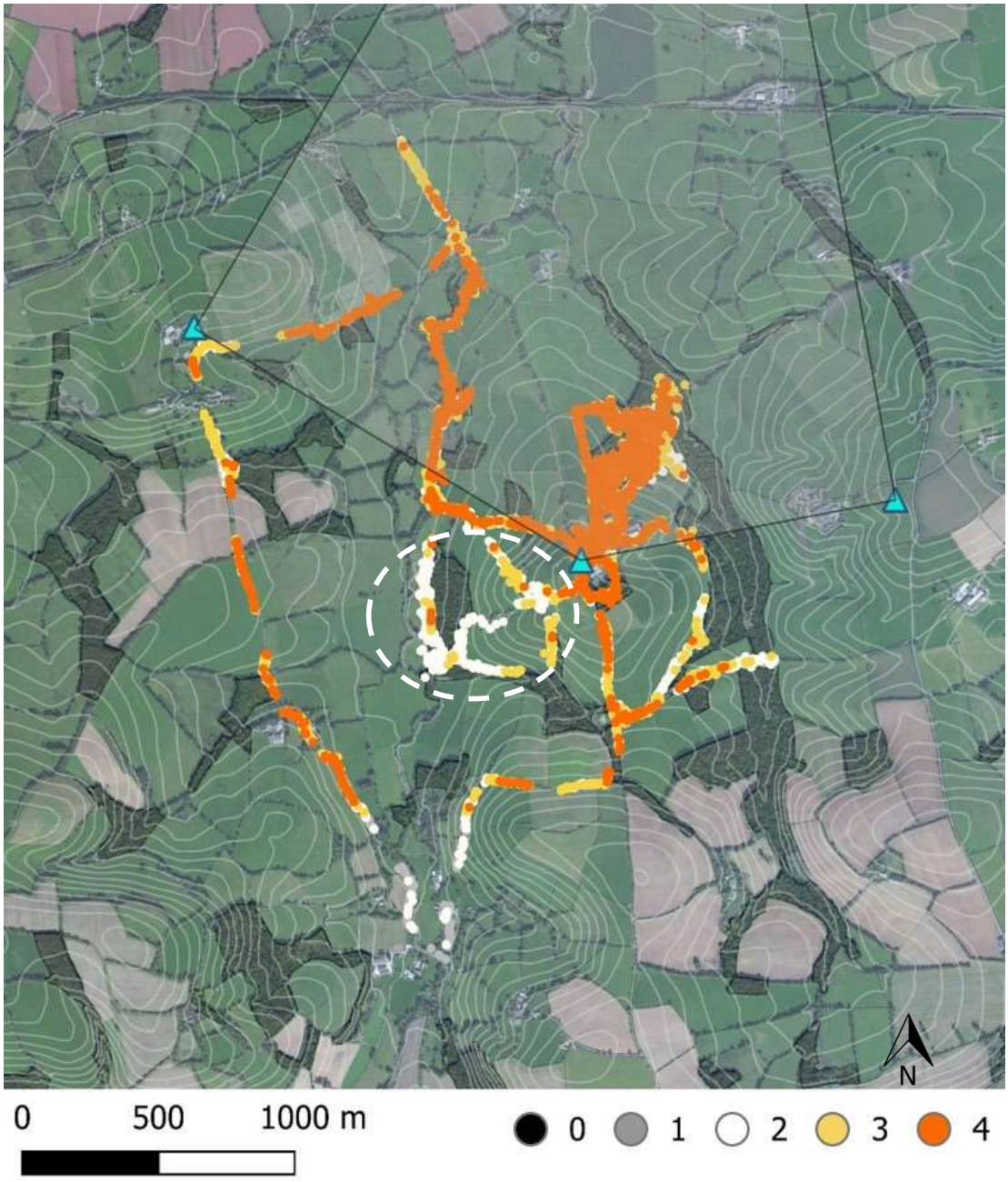


Figure 4.10 Coverage of the receiver station receivers (blue triangles) around our field site for moving tags. Orange circles show GPS locations. Colour denotes the number of receiver stations that detected an ATLAS tag within 4 seconds of the GPS timestamp. Gaps in a clear path of GPS routes indicates that GPS did not find fixes in these areas. White dashed oval illustrates an area where we have very poor coverage.

Table 4.2 Moving tag experiment performance of GPS and ATLAS. Fix rate indicates the number of fixes divided by the total possible number of fixes at 1Hz (GPS) or ¼ Hz (ATLAS).

Trial	*Seconds on route*	*Actual GPS locations (fix rate at 1 Hz)*	*Actual GPS sample interval in seconds (mean ± SD [range])*	*Mean Number of Satellites ± SD*	*ATLAS localisations (fix rate at ¼ Hz)*	*ATLAS tag detection intervals (mean ± SD [range])*	*Mean number of receiver stations ± SD*
T1	9300	2666 (28.7 %)	3.49 ± 0.849 [2-11]	10.22 ± 2.02	1360 (58.50%)	3.97 ± 1.32 [3.99-52.00]	2.76 ± 0.98
T2	3598	1029 (28.6 %)	3.5 ± 0.89 [1-10]	10.27 ± 1.87	808 (89.83%)	3.96 ± 0.42 [3.98-4.00]	3.37 ± 0.71
T3	14099	3963 (28.1%)	3.56 ± 0.88 [2-20]	9.80 ± 1.90	2584 (73.31%)	4.02 ± 1.24 [3.99-36.00]	2.99 ± 0.98
T4	3108	389 (12.5 %)	8.01 ± 2.37 [1-21]	8.87 ± 2.01	300 (38.61%)	2.91 ± 1.41 [0.862-8.00]	2.07 ± 1.01
T5	2950	594 (20.1%)	5.08 ± 1.90 [1-23]	8.01 ± 2.09	671 (90.98%)	4.00 ± 0.00 [3.99-4.00]	3.54 ± 0.64

4.4.2.3 Pheasant field test

After combining and visualising all filtered data collected from our 2017-2018 field season, we could visualise a ~3 km diameter site within which pheasants could be reliably located and hence tracked, centring near our release pen (Fig. 4.11). The service area extends ~ 2 km further north than our pheasant tracks show, but these seem to stop at a train track that runs through our study area. Much of the northern service area is within a valley which may not be visible to the receiver stations or alternatively may be avoided by the birds. We were unable to include this area in the moving tag experiment as the majority of the area is private land or busy roads. Finally, from our most southerly receiver station, there seems to be straight lines of locations that seem to follow the projections of the receiver station alignments (length = ~2.5 km) and which are unlikely to be made by birds, although birds may be responsible for a few of the locations (Fig. 4.11). These perceived errors were not removed by the filters and were removed manually using QGIS (QGIS Development Team, 2017).

4.4.3 Accuracy and Precision

4.4.3.1 Moving Tag Experiment

Relative to locations determined using GPS, unfiltered localisations generated by ATLAS showed high levels of variation suggesting that they were typically of lower precision. The region in which our pheasants are released and spent most of their time in the first few months (< 450 m from centre of release pen) had a median accuracy (difference in m from GPS localisation) of 46.19 m [n=2486, CI:44.90-48.01]. We found three factors influenced the accuracy of ATLAS. Localisations calculated with 4 receiver stations were more accurate than localisations calculated with 3 receiver

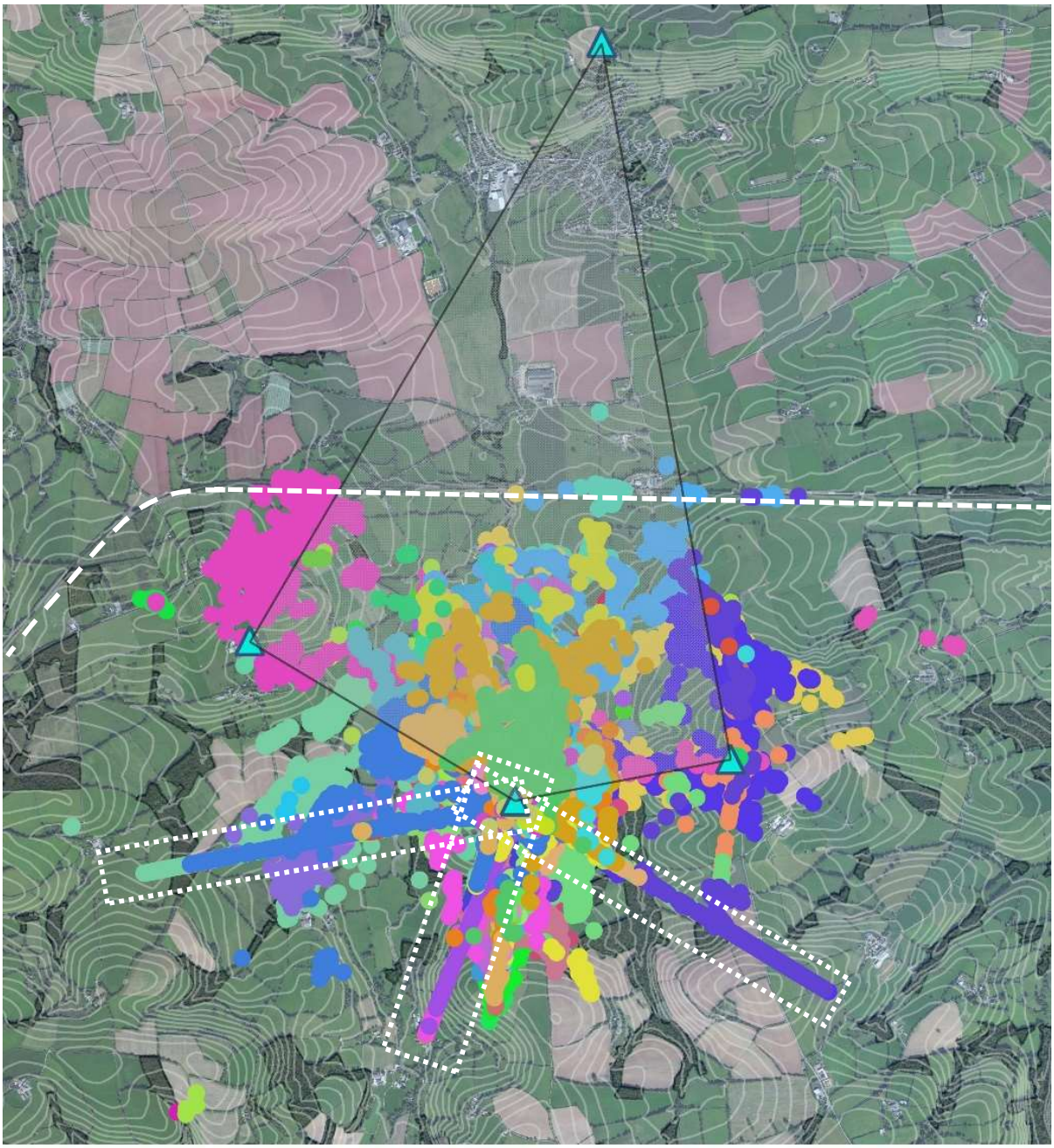


Figure 4.11 All locations recorded from 184 individual pheasants between 27th July 2017 and 1st Feb 2018 (total data points = 857,600). White dashed line denotes a railway track that runs through our study area. White dotted boxes indicate unnatural localisations seemingly emitted from the most southern receiver station. Blue triangles are receiver stations and are connected to show likely service area of the system. Contours show 5 m height intervals. Individuals are denoted by different colours.

more accurate than those collected from Open (β ± SE = -0.898 ± 0.073, p <0.001) or Urban (β ± SE = -0.684 ± 0.128, p <0.001) habitats but there was no difference between Open and Urban habitats (β ± SE = -0.214 ± 0.127, p = 0.093). Locations

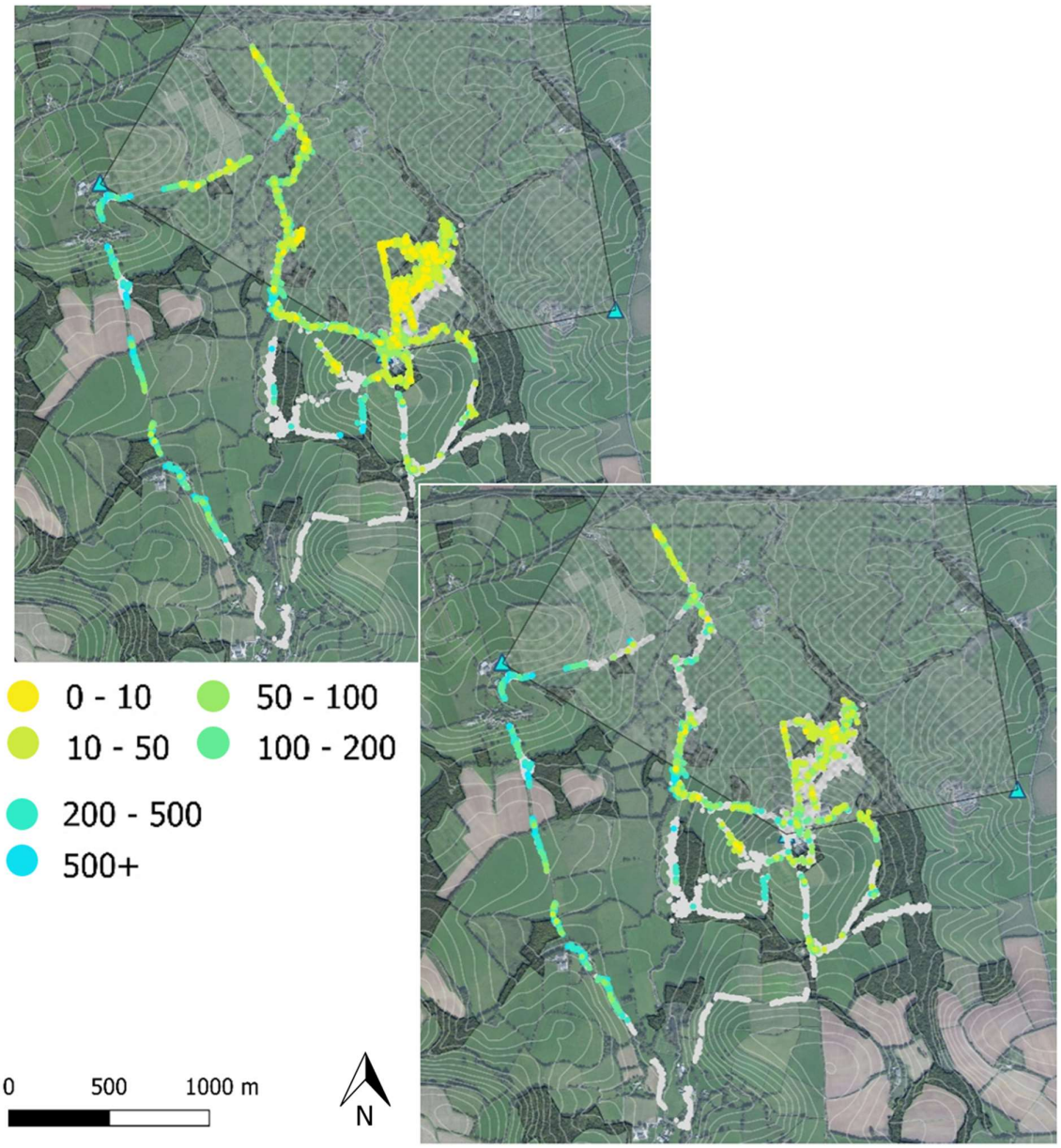


Figure 4.12 GPS positions in experiment 1 for a moving subject (grey) overlaid with colour that denotes the distance between GPS and ATLAS positions that are recorded as being 1 second or less apart. Yellow (accurate) – blue (inaccurate). Service area for all 4 receiver stations shown by lines connecting blue triangles. a) Raw data b) VarXY Filtered data – all points with variance in x or y of > 75 removed. Contours are 5 m.

collected from the interior of the service area were more accurate than the exterior (β ± SE = -1.167 ± 0.088 p < 0.001) (Table 4.3).

Table 4.3 Summary statistics for distances between GPS and ATLAS tag positions depending on service area, number of receivers and habitat type. Raw data is from the ATLAS system. VarXY Filtered data has been selected to only include positions with less than 75 variance in the x and y axes which is the first step in our filtering process. Other filters could not be included as the time stamps may not be matched appropriately after pooling into 5-minute time periods.

Data type	*Service Area*	*Number of receivers*	*Habitat*	*N*	*Median (m)*	*Mean (m)*	*SD*	*Range (m)*
Raw	Interior	3	Woodland	544	45.646	59.362	146.965	1 - 3360
VarXY	Interior	3	Woodland	512	45.021	50.727	33.858	1-273
Raw	Interior	4	Woodland	943	36.661	42.568	29.651	1-333
VarXY	Interior	4	Woodland	942	36.629	42.504	29.601	1-333
Raw	Interior	3	Open	583	80.194	208.666	729.633	3-8699
VarXY	Interior	3	Open	412	70.211	96.201	98.413	3-1173
Raw	Interior	4	Open	740	78.778	93.897	73.411	1-450
VarXY	Interior	4	Open	725	77.613	91.751	69.794	1-450
Raw	Interior	3	Urban	79	65.353	93.414	91.896	4-645
VarXY	Interior	3	Urban	71	60.430	79.842	58.323	4-286
Raw	Interior	4	Urban	188	74.411	88.751	58.815	4-318
VarXY	Interior	4	Urban	188	75.511	88.751	58.815	4-318
Raw	Exterior	3	Woodland	47	215.955	440.038	818.185	18-4311
VarXY	Exterior	3	Woodland	26	93.087	154.881	126.796	18-550
Raw	Exterior	4	Woodland	70	59.097	150.499	257.597	2-1631
VarXY	Exterior	4	Woodland	58	53.771	68.967	68.967	2-405
Raw	Exterior	3	Open	369	217.418	519.317	1204.192	4-15616
VarXY	Exterior	3	Open	164	111.947	193.798	194.086	4-941
Raw	Exterior	4	Open	231	164.025	277.167	321.737	2-2581
VarXY	Exterior	4	Open	125	90.742	117.345	117.345	2-401
Raw	Exterior	3	Urban	18	299.129	411.848	423.092	50-1631
VarXY	Exterior	3	Urban	5	69.961	72.445	18.232	50-98
Raw	Exterior	4	Urban	26	176.043	365.621	469.585	56-2194
VarXY	Exterior	4	Urban	15	88.723	107.851	51.600	56-241

4.4.4 How did filtering influence accuracy and precision?

4.4.4.1 Moving Tag Experiment

For most of the landscape we tested (see Table 4.3 for different combinations of service area (Exterior/Interior), number of base stations (3/4) and habitat type (woodland/open/urban)) median accuracy was improved from the raw data by using our first filter, VarXY (mean = -53.25 m; min = 1.1 m; max = -229.17 m; Table 4.3). We did not test our median or speed filters on moving tag data since the experimenter moved too far over 5 minutes to give a reliable comparative location from GPS. All areas improved in precision, measured by the standard deviation of errors between raw and VarXY filtered data.

4.4.4.2 Stationary Tag Experiment

In the stationary tag experiment, the filters removed most inaccurate localisations from the dataset and increased precision dramatically (Table 4.4). However, the filters had no impact on the accuracy of the 50th percentile ATLAS-derived locations (V = 44, n = 11, p = 0.365; Table 3). However, the accuracy of the 95th percentile of data improved with filtering (V = 66, n = 11 p = 0.001). One important point to note is that the localisations for three tags (Table 4.4 ref: I, M, N) that were estimated to be inaccurate by more than 100 m did not improve and were not removed by the filters. This is problematic and would therefore be false positive localisations in a real-world scenario that would be unlikely to be noticed. The precision (standard deviation) around the estimated points decreased between the raw data and fully filtered data (V= 65, n = 11, $p < 0.01$; Fig. 4.13, Table 4.4).

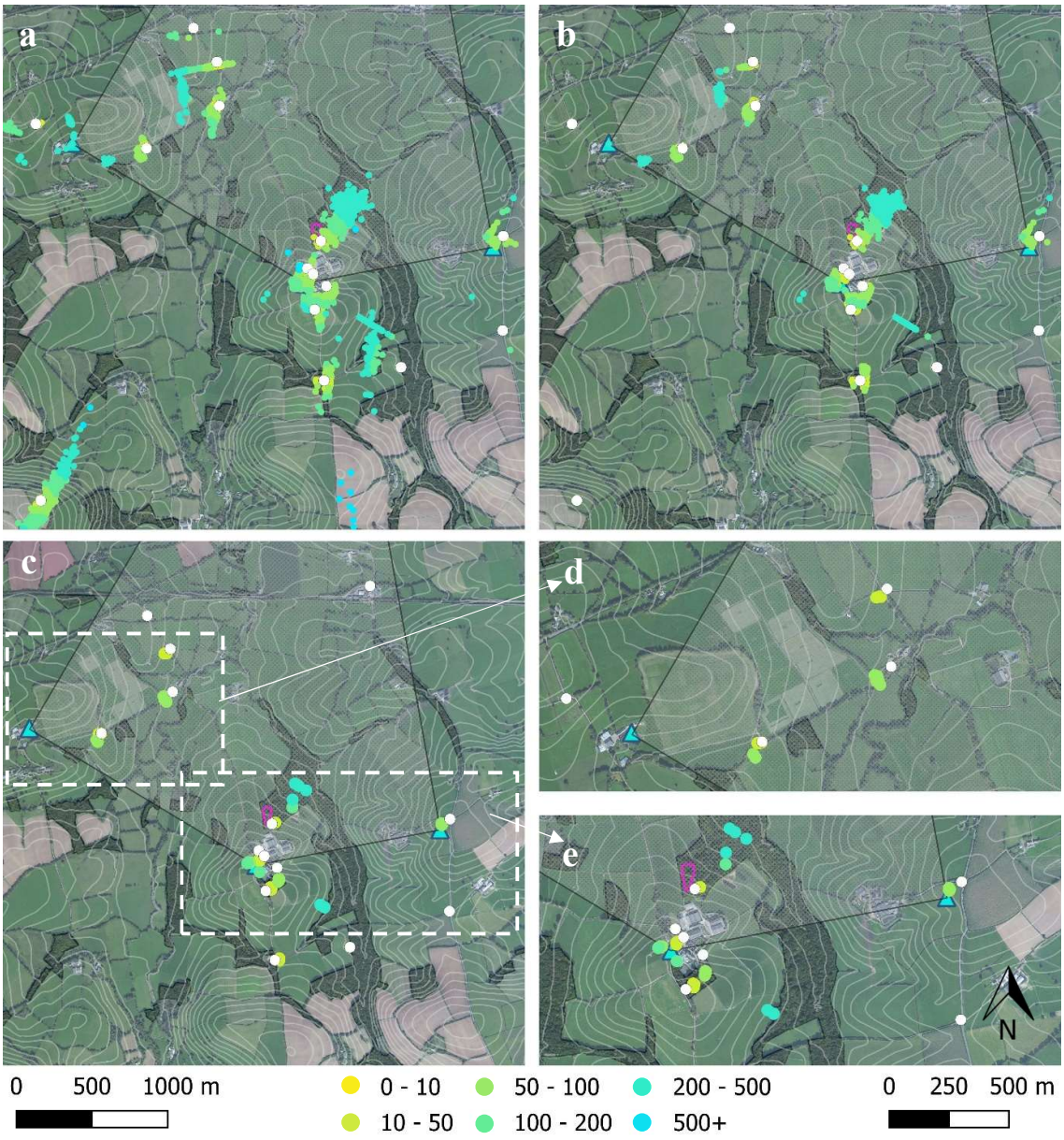


Figure 4.13 White circles denote locations of tags in fixed locations. Circles that lie on colour gradient of yellow (0-10 m accuracy to blue (500+ m accuracy) shows the ATLAS derived locations from a)Raw data b) Var XY filtered data; c-e) 5 minute median filtered data (e-f zoomed) whereby accuracy of point is denoted by colour (see legend).Shaded polygon indicates the service area of the 4 receiver stations. Left scale bar is a reference for maps a-c; right scale bar is a reference for d-e

Table 4.4. Stationary tag experiment results. Stationary tags were placed in locations differing in habitat and service area for 30 minutes. Receiver station reliability is demonstrated by noting the number of receiver stations that detected each transmission from the tag. Accuracy (the maximum distance from the true location of 50 % and 95 % of the data) is displayed for raw data and data filtered from VarXY filter and the median filter (5-minute medians of VarXY filtered data). The speed filter had no impact therefore the results are not shown. 'Ref' denotes location which can be found on Figure 4.6.

			Detections of tags by 1-4 receiver stations				Accuracy (Distance (m) from true location -50th & 95th Quantile for location error)						Precision (m) (Standard Deviation)		
Ref	**Habitat**	**Service Area**	**One**	**Two**	**Three**	**Four**	**Raw (q50)**	**VarXY filter(q50)**	**Median Filter (q50)**	**Raw (q95)**	**VarXY Filter (q95)**	**Median Filter (q95)**	**Raw (SD)**	**VarXY Filter (SD)**	**Median Filter(SD)**
A	Open	Interior	2	16	45 (9 %)	397 (86 %)	15	11	15	245	245	58	62	62	25
B	Open	Exterior	6	10	19 (4 %)	425 (92 %)	32	31	28	79	62	30	46	13	2
C	Open	Exterior	8	3	65 (14 %)	383 (83 %)	42	41	40	80	69	41	17	12	3
D	Building	Interior	16	82	282 (61 %)	79 (17 %)	45	39	39	176	134	89	44	36	27
E	Open	Interior	4	69	118 (25 %)	264 (58 %)	47	45	38	212	209	47	56	53	7
F	Open	Exterior	2	6	7 (1.5 %)	440(96 %)	64	64	62	91	91	64	16	16	2
G	Open	Interior	4	14	201 (44 %)	234 (51 %)	70	70	66	236	230	73	60	53	6
H	Open	Exterior	15	13	64 (13 %)	377 (80 %)	74	74	73	111	111	86	18	17	7
I	Open	Interior	12	6	16 (3 %)	431 (92 %)	100	100	99	117	117	106	19	19	5
J	Building	Exterior	10	20	48 (10 %)	381 (83 %)	111	NA	NA	331	NA	NA	177	NA	NA
K	Open	Interior	36	416	1 (0.2 %)	0	134	NA	NA	155	NA	NA	34	NA	NA
L	Open	Exterior	12	442	1 (0.2 %)	0	203	NA	NA	272	NA	NA	107	NA	NA
M	Woodland	Interior	16	54	172 (37 %)	218 (47 %)	226	209	246	345	332	298	103	103	108
N	Open	Exterior	83	164	161(35 %)	51 (11 %)	289	310	323	1079	356	325	250	30	15
O	Open	Exterior	9	15	185 (40 %)	250 (54 %)	497	315	NA	5623	368	NA	2298	83	NA
P	Open	Interior	219	198	0	0	NA	NA	NA	NA	NA	NA	NA	NA	NA

4.4.4.3 Pheasant field test

Application of the filters to 4 real pheasant tracks improved the precision of the tracks. We do not have truthing data for any of these bird's movements, so we cannot consider improvements in their accuracy. While many large 'jumps' and outliers were removed by the VarXY and median filters in 3 of the tracks, one track (Individual 4, Fig. 4.14) had some 'jumps' remaining which were subsequently removed by the speed filter. Visual assessment of the tracks of the pheasants indicate that raw data is less error prone within the service area but that the filters were especially effective at reducing this error if the tag was slightly outside the service area; this is particularly evident for individual 4. Inspection of the tracks of real birds revealed that they behaved in ways that we might expect from our direct observations of them, with birds spending time clustered round artificial feeder sites, following liner features (hedges/fences/woodland boundaries) and spending little time in exposed open fields (Fig. 4.15).

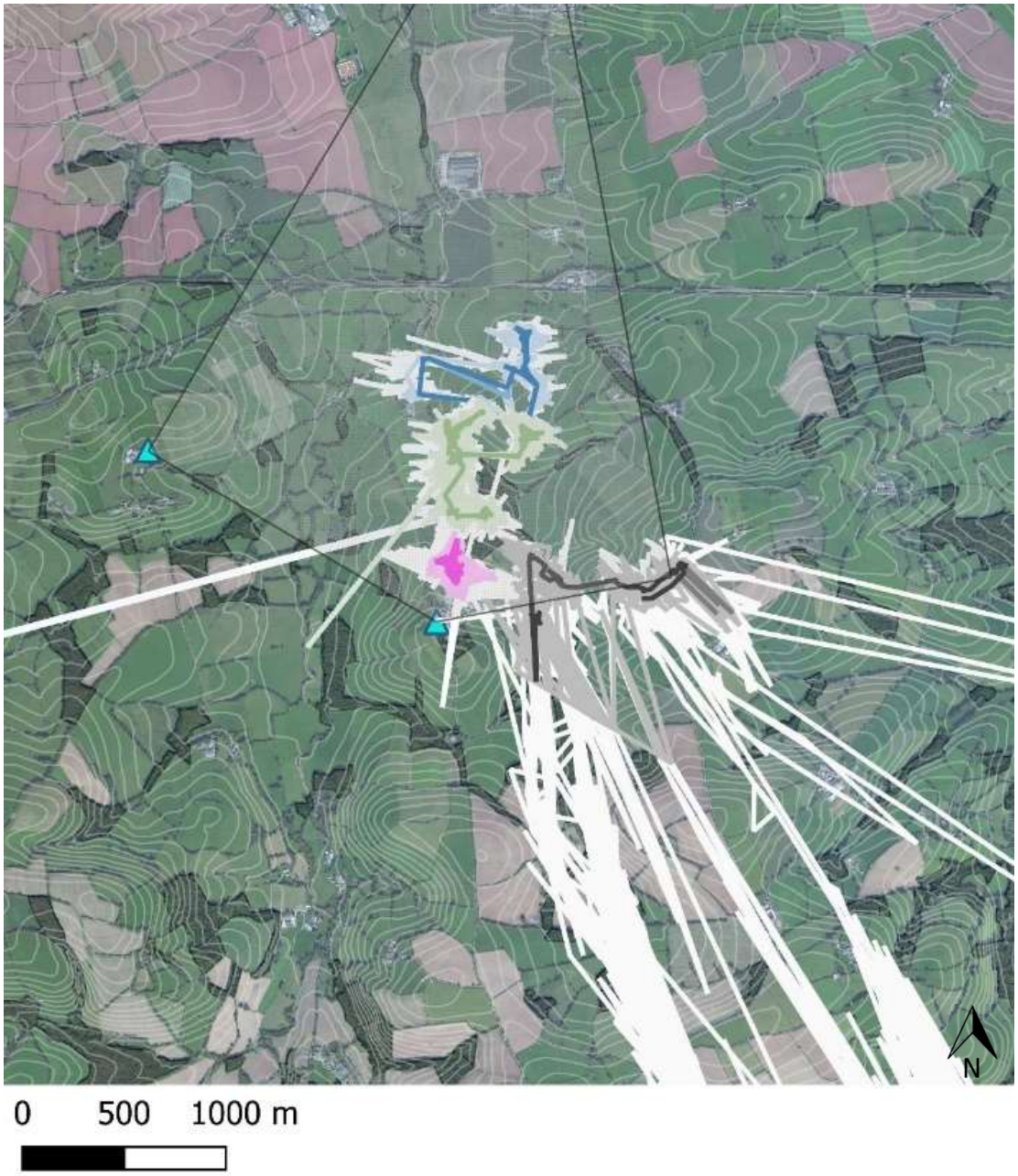


Figure 4.14 Tracks of 4 individual pheasants over 1 day (separate days) demonstrating the filter efficiency on real organisms as they move within the receiver station boundaries. Raw data (white) is smoothed through the 3 filters sequentially (Variance in X & Y < 75 = light; 5-minute median = medium colour; speed < 0.5 m/s = darkest colour). Colours are unique to the individual (Individual 1 = blue; Individual 2 = Green; Individual 3 = Pink; Individual 4 = Black.

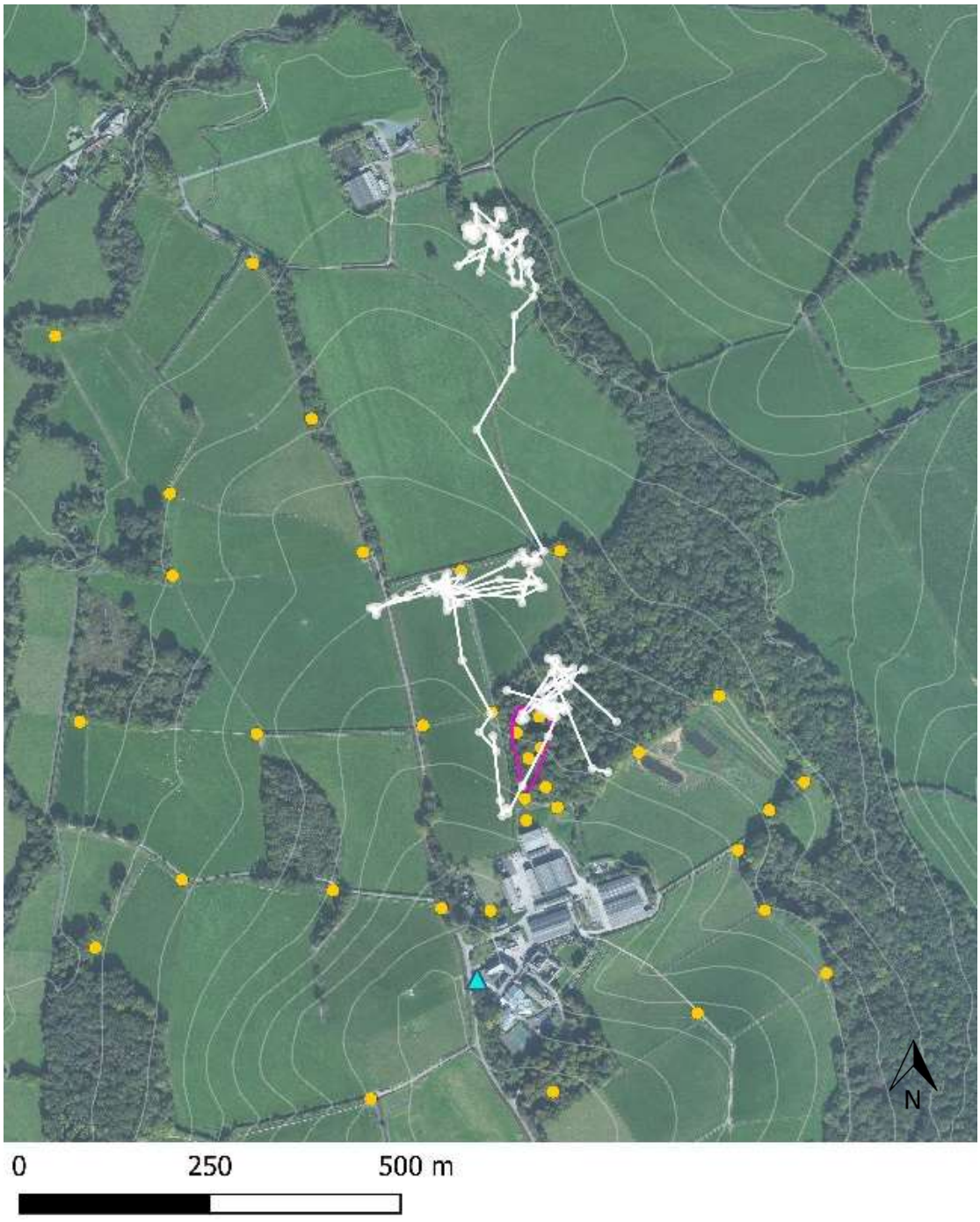


Figure 4.15 Example of one individual's filtered track (15th October 2017) as it moves between feeders and across a field following a path. This demonstrates a pheasant performing naturalistic behaviours: following a linear feature (a farm track), visiting several feeders (yellow circles) and crossing a field while following a fence line. This is a highly likely scenario for a pheasant and gives us faith in the accuracy of the system while on a real bird.

4.5 Discussion

We found that a novel reverse-GPS tracking system, ATLAS, performed reasonably well at our study site. It had good coverage of the area and we could reliably detect tags ~99% of the time (at a level better than provided by GPS). Although coverage and detection rates were good, the rate of localisations was less satisfactory (~70% of all detections produced a localisation), probably because this required detections from ≥3 receiver stations and the hilly nature of the site meant that with only a few receiver stations, some areas were concealed from sufficient receiver stations. When we did obtain localisations, raw localisations differed from simultaneous GPS locations by a mean of 46 m. However, this accuracy improved within the centre of our array area and could be further improved by applying our sequence of filters. Filtering also greatly improved precision of localisations. This filtering of raw data produced movement tracks from free-moving birds that conformed to naturalistic behaviours that we commonly observed directly.

We found that almost all transmissions from ATLAS tags in our moving tag experiment were detected by at least one receiver station. ATLAS even detected transmissions in GPS blind spots, yielding approximately 10 minutes of detections where GPS gave no localisations. With such a high detection rate from ATLAS receivers, ATLAS could outperform GPS for coverage in this area. However, three or more receivers are required to detect the same transmission to be able to multi-laterate and estimate a location therefore, although the detection rate was high, only 69.26% of tag transmissions were localised. It is important to note also that our GPS tag likely has a filtering method that precludes

localisation with fewer than a set minimum of satellite detections (Lewis, Rachlow, Garton, & Vierling, 2007), therefore in GPS blind spots, the receiver may have actually detected a small number of satellites which did not result in a localisation. We found one area of our field site to be particularly difficult for ATLAS to generate localisations. This was a valley approximately 700-1000 m South West of our release site. This is problematic as in previous years we have directly observed and automatically photographed pheasants in this area (Whiteside et al., 2019). Although we obtained reliable detections of tags known to be in this area from two receiver stations, our other receiver stations could not detect tags there. We conclude that a carefully placed 5th station could cover this area and supply the essential third simultaneous detection to generate localisations. We noticed, after visualising seven months of ATLAS-derived location data from free-roaming pheasants, that we obtained no localisations from a segment of the northern part of our assumed service area. We suspect that the northern area is either a blind spot for our current system, perhaps due to the valley that is present within this area or alternatively, that pheasants may not have crossed the railway track that runs through this area. Since only four birds were detected near the railway track, both scenarios are feasible. We were unable to assess the northern area of the field site effectively as part of our truthing experiments due to land access restrictions.

During our first experiment, we assessed the accuracy of the ATLAS system based on estimated locations from the GPS of a handheld android smartphone. Unfortunately, we found this GPS to be relatively unreliable. First, the unit reported localisations at ~3 Hz suggesting that ~2/3 of locations were not logged because we had set the sampling rate to 1 Hz. This is not an uncommon

phenomenon, with other studies reporting problems with GPS fix rates, especially when tracking free-roaming animals (Edenius, 1997; Schwartz, Podruzny, Cain, & Cherry, 2009; Yamazaki et al., 2008). However, when comparing to ATLAS the lower than expected fix rate of GPS was not a problem as the ATLAS tag itself was only set to ¼ Hz. Secondly, the GPS had approximately 10 m error when compared to dead reckoning against known conspicuous landmarks encountered on our experimental routes, even in open environments. We were unable to assess the location error of the GPS in woodland or around farm buildings because we could not identify these conspicuous landmarks in these habitats, but we expect error to be even higher in these areas based on the findings of previous studies (Edenius, 1997; Yamazaki et al., 2008). For instance, in suburban environments, GPS has been shown to have a mean location error of 30.1 m (Adams, Dickinson, Robertson, & van Heezik, 2013). While GPS was effective in open areas, a more accurate assessment in woodland or urban areas that could be used in future studies is to physically mark the route taken and follow this route multiple times, negating the requirement for GPS to calculate the route taken. Other studies have used measures of precision as a proxy for accuracy (Weiser et al., 2016). Despite our issues with the GPS unit, the precision in our ATLAS system was, in many cases, equal or better than that reported in some GPS studies, especially for filtered data, when we could obtain a precision of ~2 m in some places). This provides encouraging evidence that with more receiver stations, a highly accurate and precise system can be obtained, even within a hilly and potentially difficult to monitor landscape. Finally, it is useful to note that we compare a GPS unit that frequently obtained fixes with more than 2-3 times the number of receivers than the ATLAS system, but even with only 4 receivers, some of the ATLAS locations shown by free-roaming pheasants were

compelling (see Fig. 4.13B for an example of a pheasant following a path and fence line).

The importance of careful selection for the locations of ATLAS receiver stations was evident from our study. We selected sites based on the line of sight from the receiver station to our release pen, which resulted in the release pen being one of the most accurate areas of our study site. We found that the most accurate locations were produced within the service area. This is similar to Kays et al. (2011) who found that accuracy decayed closer to the periphery of their receiver array. Anecdotal evidence from other ATLAS systems (personal communication) suggests this is a common trait. Detections by more receiver stations also produced more accurate localisations. Again, this is unsurprising and GPS technology has long used the minimum number of satellites detected as a basic filtering mechanism, since locations produced with few satellites are less accurate (Yamaguchi & Tanaka, 2006). We found no difference in accuracy between tags placed in open and urban areas. We also showed that our system produced more accurate locations in woodland than in open or urban habitats. We believe that this particular result is, at least in part, due to the location of the main woodland in which we tested which was in line of sight of our receiver stations. However, this also indicates that habitat is not a limiting factor for our ATLAS system as woodlands are notoriously difficult habitats for radio-telemetry methods, since radio-waves are scattered and absorbed by foliage, affecting signal strength (Kays et al., 2011).

Our sequential filtering increased both the accuracy and precision of ATLAS localisations. Filters also completely removed extreme outlying, likely inaccurate sets of locations, allowing for a reduction in false positive (type I) localisations. This will give us confidence that, although we may have a smaller area in which the system gives locations (~3 km), the locations that remain are relatively accurate (maximum filtered 95th percentile of error for all stationary tags was 325 m as opposed to 5.6 km of the raw data). Despite these results, we were unable to remove erroneous location estimates (>100 m) for three stationary tags. One of these tags was situated directly under a tree in woodland (Fig 4.6 M) and had low accuracy and precision even after applying all filters. This may mean that resting animals may be construed as moving while in woodland. For the other two problematic stationary tag locations (Fig 4.6: I and N), the precision of the filtered data was high, therefore it is likely that some reflection occurred. For pheasants (and other moving animals) both of these types of error may be most harmful to datasets when the animal is stationary as for moving animals a speed filter should remove reflective errors.

Speed filters have been shown to be useful in other GPS studies to eliminate outliers (Bjørneraas et al., 2010; Patterson et al., 2010). We did not run the speed filter on the human-based experiments as our speed threshold was based on pheasant movement. However, when applied to the four, individual free-roaming pheasants, the speed filter removed several sudden and biologically unlikely jumps (see Figure 4.13A: white-black individual) indicating that its inclusion was very useful. While the filters increase both accuracy and precision of our location data, there is a cost in terms of temporal resolution. The median filter reduces the resolution of the data by summarising up to 75 localisations into a single measure.

For faster moving species this could be problematic and more complex methods might be more suitable. Kalman filters (Kalman, 1960) have proved to be highly effective for a number of ARGOS and GPS studies (Patterson et al., 2010; Sibert et al., 2003; Stoew et al., 2001; Yamaguchi & Tanaka, 2006). However, Kalman filters are sensitive to non-Gaussian errors and outliers (Wikle & Berliner, 2007), to which median filters are robust. We therefore feel that our filtering method is suitable for our system. We found some reflective errors that were not removed by our filters. These manifested as straight lines over ~200 m originating from one of our receiver stations. We found that these errors were easily identified and dealt with by plotting large portions of data at once so that they could be removed manually using GIS software.

At a cost of ~£15 per bird (compared to >£1000 for GPS), ATLAS provides a cheap alternative to satellite tracking systems with numerous benefits. Firstly, simple and continuous data retrieval options enable researchers to relocate lost tags through a desktop visualisation application and furthermore determine the fate of individuals. Secondly, the lightweight nature of the tag means that smaller species are able to be tracked and, as a further consequence of the lighter tags, larger (and therefore longer lasting) batteries can be added to elongate the life of the tag. Thirdly, high temporal resolution can be traded for higher spatial resolution through simple filtering methods in more difficult landscapes. Although there are currently areas within our field site that seem to be blind spots, we are confident that more receiver stations would produce a more complete and accurate picture of movement and that ATLAS is therefore a suitable choice of tracking system for the studies within this thesis.

5 The speed and straightness of transitory paths in young birds released to a novel environment relates to accuracy in a spatial cognition task

5.1 Abstract

The ability to remember spatial information is expected to determine an individual's movement patterns around the landscape. However, empirical demonstrations of links between inter-individual variation in spatial cognitive ability and the development and structure of movement paths are lacking. We assessed the spatial cognitive ability of young pheasants (*Phasianus colchicus*) before releasing them into a novel, rural landscape and tracking their movements so that we could quantify changes in the straightness and speed of their transitory movements as their experience increased. Birds with better early-life spatial cognitive ability initially moved between patches more slowly than their poorer performing counterparts, but there was no difference after one month of tracking. All individuals increased the straightness of their transitory paths over time, but we did not detect any differences between individuals according to their spatial cognitive ability. We suggest that different cognitive styles (slow-accurate, hasty-inaccurate) may shape movement decisions in novel environments.

5.2 Introduction

Reducing the time and energy spent searching for resources can help animals maximise their foraging efficiency and reduce their exposure to predators (McNamara & Houston, 1987), such that even small increases in the efficiency of movements can accumulate across a lifetime thus bringing fitness benefits (Fagan et al., 2013). There are marked individual differences in patterns of movement behaviour (Chapman et al., 2011), which can be highly repeatable (Campioni et al., 2016; Patrick et al., 2014). These within-species differences have recently been shown to explain more variation in movement than differences between species (Harrison et al., 2019). An individual's spatial cognitive, namely the ability to collect, process, store and utilise spatial information has been suggested to influence movement decisions (Bracis et al., 2015; Nathan et al., 2008) and thus improve their movement efficiency. This ability of an individual can be assayed in both laboratory (Pravosudov et al., 2005; Sanford & Clayton, 2008; Sewall et al., 2013) and wild populations (Croston et al., 2016; Shaw et al., 2015) and performances on tasks assaying this trait have been correlated with proxies of fitness including better survival (Maille & Schradin, 2016a; Sonnenberg et al., 2019), increased sexual success (Shohet & Watt, 2009; Smith et al., 2005) or reproductive investment (Branch et al., 2019; Shaw et al., 2019). However, to our knowledge, few studies have demonstrated the seemingly obvious link between spatial cognitive ability and movement behaviour, namely that spatial cognitive ability corresponds to the efficiency of movement between areas of interest such as foraging patches or refuges in both the rate of development of paths and the overall efficiency of movement.

Differences in inter-individual spatial cognitive ability can be assessed under controlled conditions by adapting well-established methods used within comparative psychology. Tasks that simulate foraging can comprise food being hidden within a set of potential locations (Saleh & Chittka, 2007; Sutherland & Gass, 1995) frequently arranged as a grid (Sanford & Clayton, 2008) or radial maze structure (Olton & Samuelson, 1976). Success in these tasks can be achieved by learning and remembering which location(s) offer a reward. By counting the number of errors made before attaining the reward and assessing performance over multiple trials, researchers can quantify an individual's spatial cognitive ability (e.g. Astié *et al.* 1998).

Quantifying individual movement in real-world landscapes demands high spatial and temporal resolution tracking, with individuals being followed continuously over extended time periods and their location being logged every few seconds, minutes or hours, according to their typical movement speeds and distances travelled (Patrick & Weimerskirch, 2014; Votier et al., 2011). This permits an individual's path to be described both spatially and temporally. If measures from the same individual can be collected repeatedly over time, then their improvements in efficiency as indicated by a decrease in time taken (i.e. speed), path length or tortuosity of path between two locations (Bartumeus et al., 2016) can be established. Crucially, to measure improvement in movement efficiency, it is essential that the prior experience of the individual in that environment is known and accounted for. This means that a naïve individual should be tracked from the first time that they enter a landscape, otherwise older or more experienced individuals may appear to be more efficient simply because they have more knowledge of that environment. Additionally, it is desirable to account

for the effects which more experienced individuals (e.g. parents) may have on the development of a focal individual's movement through leadership or followership. Naïve individuals may accompany others with prior knowledge of the landscape, which could help them to develop more efficient routes (Mueller, O'Hara, Converse, Urbanek, & Fagan, 2013; Pettit, Flack, Freeman, Guilford, & Biro, 2013).

The pheasant, *Phasianus colchicus,* provides an established model for measuring individual differences in cognitive abilities (Madden, Langley, et al., 2018; van Horik, Langley, Whiteside, Laker, et al., 2018; van Horik, Langley, Whiteside, Beardsworth, et al., 2018). These differences can arise due to early-life rearing conditions (Whiteside, Sage, et al., 2016) and have fitness consequences in terms of survival (Madden, Langley, et al., 2018). Their annual *en masse* release as a managed game bird in the UK, coupled with their large size and relatively sedentary nature, provides an unusual opportunity to explore how spatial cognitive ability may relate to movement in a free-roaming terrestrial bird. Pheasant chicks are precocial and can therefore be reared without parents, removing opportunities for inter-generational learning. They can be housed under controlled conditions for several weeks, removing differences in cognitive abilities caused by variation in early-life experiences. Crucially, they can be introduced into the wild, allowing their movement in naturalistic landscapes to be recorded. Because entire cohorts are released simultaneously and at the same location, all birds are naïve to the environment at the point of release and have equal opportunity to explore the same area with exposure to the same distribution of resources and threats. Birds are limited in access to informed individuals who they could follow, since adults are caught for breeding and released elsewhere.

Pheasants therefore provide a useful model to study the influence of cognitive traits on the efficiency of individual's movement paths in natural landscapes.

We assayed the spatial cognitive ability of a cohort of pheasant chicks while controlling for age, experience and environment, using a five-arm radial maze with a single baited arm. We released these birds as part of a soft-release protocol (as in Madden *et al.* 2018; Whiteside *et al.* 2018a) and monitored their movements using the reverse-GPS System, ATLAS (Weiser et al., 2016). Tortuous paths are costly (Amélineau et al., 2014; Wilson et al., 2013) and as individuals become familiar with a landscape, their trajectories between places of interest have been demonstrated to increase both in straightness and speed (Carter et al., 2019; Osborne et al., 2013). We isolated sections of trajectories where birds were in transit between places of interest, such as foraging patches or resting locations using a hidden-Markov model. We assessed whether the early-life spatial cognitive ability of an individual predicted the straightness and speed of their transitory paths after release into the wild or improvements in these measures. We do not expect pheasants to optimise their transitory paths to produce straight lines as pheasants rarely fly and instead, they must navigate around complex terrestrial environments, negotiating woodland or man-made structures. Instead, we predicted that birds with better spatial cognitive ability would improve the straightness (by taking more direct paths) and/or speed (by choosing easier terrain or increasing in 'confidence' of the goal location), more quickly than birds with poor spatial cognitive ability.

5.3 Methods

5.3.1 Subjects and housing

We hatched 190 chicks (87 females and 103 males) on 25th May 2017 at North Wyke Rothamsted Research farm (Devon, UK, 50º77'N, -3º9'W). They were the offspring of adults that we had caught in the wild and had released, once laying was completed, at a location 6.9 km miles away from the study site. Pheasants rarely disperse more than 3 km from release sites (Wilson et al., 1992), so our chicks would be unlikely to come into contact with their parents or other experienced individuals once released. The chicks were immediately placed into one of four indoor enclosures (1 m x 2 m) with replicated environments (perches, drinkers and food bowls) in approximately equal sized groups (2 x 47, 2 x 48). Chicks were given *ad libitum* access to age-specific commercial chick crumb (Sportsman Game Feed, London, UK) and water. At two weeks old, birds were individually labelled with numbered patagial wing tags (Roxan Ltd, Selkirk, UK).

5.3.2 Assessment of spatial cognitive ability

From 1 day old the chicks were habituated to humans by tapping the birds' food bowls allowing them to associate food with human presence. From 5 days old, chicks were shaped to enter a testing chamber (75 cm x 75 cm) from their enclosure through a sliding door, first in groups and later on their own to eat mealworms that had been scattered throughout the chamber. Chicks exited the chamber into a 'post-testing' area (0.75 m x 1.25 m) through a pulley-assisted door and were released back into the enclosure once all birds had entered the 'post-testing' area. After two weeks, the chicks were comfortable with entering and exiting the testing chamber alone and we could begin assaying cognitive

ability. For the next five weeks all birds were subjected to an identical series of cogntive tests unrelated to the current study.

At 7 weeks old, we tested the spatial cognitive ability of the pheasant chicks using a radial-maze style task (Fig. 5.1). During testing, the birds voluntarily entered the testing chamber alone and were lured to a central platform (20 cm diameter) by a dead mealworm presented in the middle of the platform. Five walls radiated from the central platform, separating the testing chamber into five compartments. At the end of four of the walls (excluding the compartment through which the birds entered the testing chamber), there was a second short wall perpendicular to the main compartment wall that obscured the view of a circular tray. In one of these trays (the location of which was consistent for all birds (Fig. 5.1)), we placed a reward of 3 mealworms, while the trays in the rest of the compartments were empty. Birds were required to walk to the end of the wall of a compartment and look around the perpendicular wall to retreive the reward. Stepping off the central platform into any of the incorrect compartments was counted as an error. Birds could not move from one compartment to another without returning to the central platform. This is an important improvement on the task used in Chapters 2 and 3 as the distance to each potential choice remains the same throughout the task, since birds must return to the centre to choose a different 'arm'. Previously (in Chapters 2 and 3), birds could have chosen to go to the nearest cup, as they could be stood anywhere in the chamber. Furthermore, the wall in front of the tray means that all birds are able to see the contents of the tray by peering around the wall from the same point. In the Cup task in chapter 2 and 3, taller birds may have been able to see into the cups from further away than shorter birds.

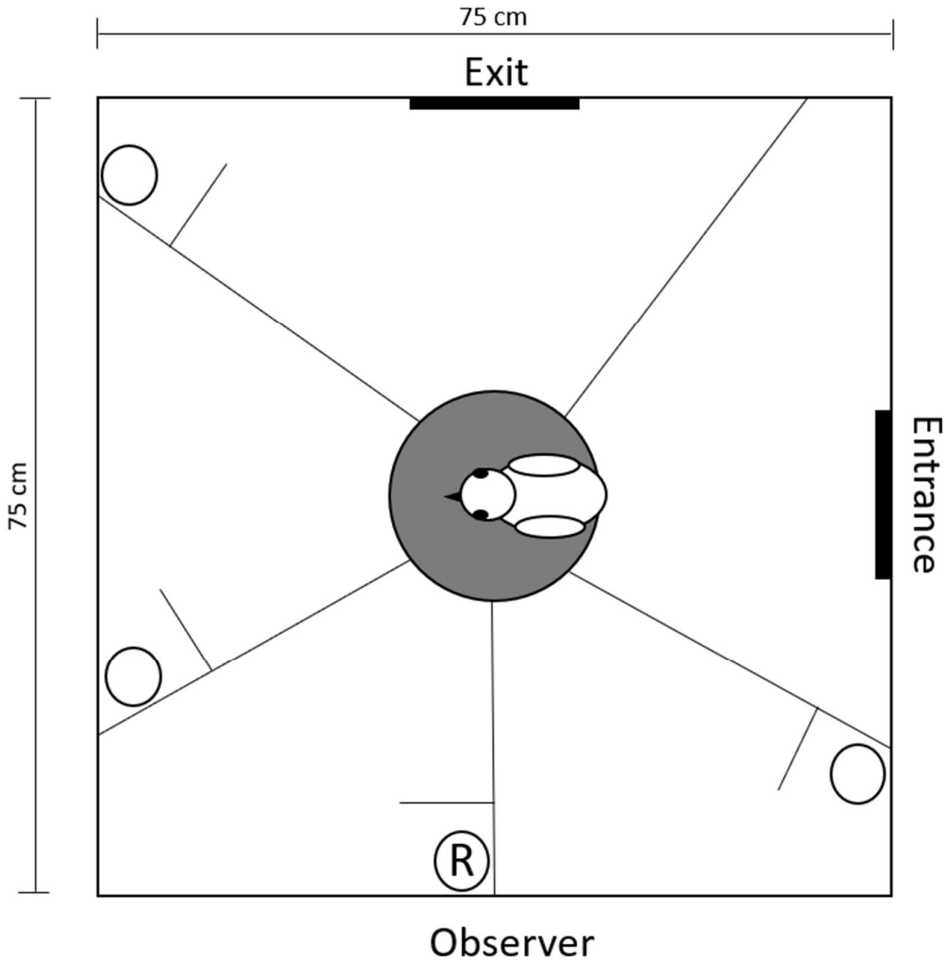


Figure 5.1 Schematic of the spatial task. Birds walk through the entrance and onto the central platform (grey circle) before beginning the task. R denotes the location of the reward (3 mealworms).

In each trial, we counted the number of errors a bird made until it retreived the reward and then immediately released it from the testing chamber. Each bird had the opportunity to complete 12 trials between 3rd -7th July 2017. The order in which individuals entered the testing chamber was also recorded in each trial. Test order has been previously found to be repeatable and is thought to indicate motivational traits (van Horik & Madden, 2016). We calculated a median test order of a bird over all 12 sessions. Birds with lower median test order could be considered more motivated by food rewards as they were consistently early to enter the testing chamber.

One hundred and sixty eight birds completed all 12 trials. A criterion based approach to assessing memory (e.g. trial number at which 10 consecutive correct response trials are completed Brady & Floresco 2015) is a popular and effective measure but requires the completion of many (sometimes hundreds) trials. Due to logistical and temporal constraints associated with assaying high numbers of young pheasants in captivity, we used a 'reverse criterion' approach. We used the maximum number of consecutive trials completed with no errors as a measure of accuracy, with birds with higher scores being assumed to have better spatial cognitive ability. This measure represents the stage of learning the bird had achieved at trial 12, with birds who had not learned the task well only completing very few no-error trials consecutively, perhaps by chance. Alternatively, birds that have a very high number of trials completed consecutively are unlikely to have achieved this by chance ($p = 0.20$ per trial), for example the probability of gaining 4 consecutive zero-error trials is $0.20^4 = 0.0016$. In order to test whether our population was performing better than chance and thus were learning the task, we simulated the performance of 50 individuals over 12 trials, whereby the probability for a zero-error trial was set at 0.2 throughout. We repeated this simulation 10,000 times and took the mean number of birds in each simulation that attained 0-12 consecutive zero-error trials to compare against the performance of our pheasants.

5.3.3 Release

The pheasants were sexed (by plumage) and weighed (Slater Super Samson spring balance – precision 5 g) when 10 weeks old on the 26th July 2017. We

fitted birds with tracking tags attached with a backpack harness that comprised elastic wing-straps threaded through heat-shrink tubing. Tags weighed 22g, which was a mean of 2.63% of released body mass (range = 2-3.67%), although birds were expected to continue to grow meaning that after a couple of months, tags were expected to weigh between 1.1% and 2.3% of adult body mass (Whiteside, van Horik, et al., 2018). We released the pheasants into a 4000 m^2 enclosure (hereafter the release pen) within a small woodland on the same farm that they were reared upon. The release pen was surrounded by a 2 m high wire fence and an additional 30 cm high electric fence to protect the birds from terrestrial predators such as red foxes, *Vulpes vulpes,* while they acclimatised to living in the wild. The release pen contained patches of vegetation providing roosting and shelter sites, as well as *ad libitum* access to water and food from feeders and drinkers. Birds typically remained within the pen for ~four weeks, but they could voluntarily leave the release pen by flying out and could return either by flying in or walking through one-way holes. During the first month, those birds that did leave the release pen were attracted back at dusk and we walked around the pen at this time to guide them back into the safety of the pen and ceased this activity on 30th August 2017. From the start of September, birds began to increasingly disperse into the surrounding landscape which consisted of a mix of grassland and woodland and contained 39 more barrel-feeders. There was no game shooting or predator control on the field site during the study.

5.3.4 Monitoring movement

We used a recently developed reverse-GPS system (ATLAS) (Weiser et al., 2016) to track the movement of the pheasants. Briefly, this system comprised a series of four synchronised, fixed base stations that recorded the time of arrival

of individually identifiable radio signals that were emitted from tags at ¼ Hz. The times were used to compute localisations for each transmission using multi-lateration. We then filtered the raw location data to compute median locations at a resolution of 5-minutes (see Chapter 4 for further details).

Due to the novelty of the system, we experienced unexpected technical difficulties which meant that our system only started recording locations of tagged birds from 17 August 2017, 22 days post-release. In addition, due to an electronics fault, we had intermittent tag transmission failures throughout the season leading to patchy location data for some dates and individuals and total loss of data for others (Fig.5.2). We confirmed 39 deaths from predation during the first two months post-release. To attempt to mitigate for these issues, we restricted our analysis

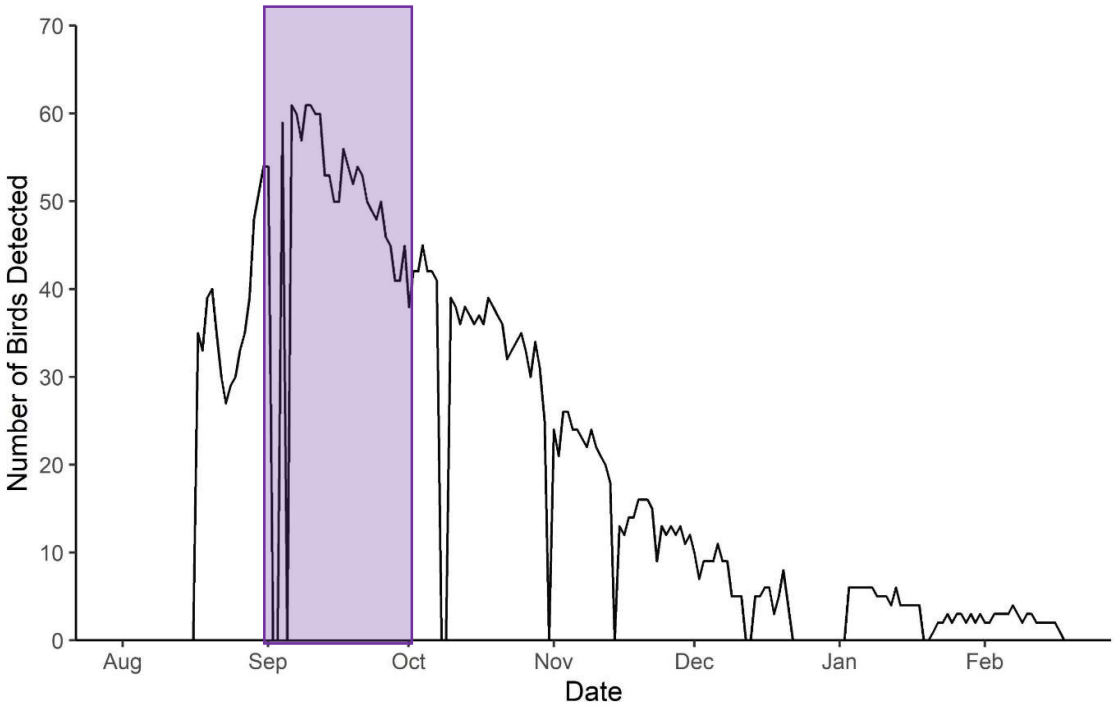


Figure 5.2 Total number of birds detected per day from release day (22nd July 2017) to the date we turned the system off (17th Feb 2018). To keep data comparable between birds and retain the maximum number of individuals we restricted analysis to September (purple box).

to movement data collected from live birds with functioning tags in September only, to ensure that data between individuals was comparable (Fig. 5.2).

We checked whether birds had explored the environment before the study period began by calculating the maximum distance travelled and the net squared displacement from the centre of the release pen for each day over all individuals and plotted the data for visual assessment. We found movements outside the release pen were initially limited (Fig 5.3) and the majority of birds remained within 200 m of the centre of the release pen between 17th August and 1st September, we therefore have assumed that this was also the case during the 22 days post-release where we are missing data. However, it should be noted that four individuals were detected > 500 m away from the release point before the 1st September. These birds return to the release pen area before September but may therefore be more familiar with the outer landscape than other birds. All birds were travelling further from the release pen in the second half of September with the mean of individual's daily maximum distances from the release pen ranging from 200 m to 500 m, although birds that performed better on the cognitive task started to explore outside the 200 m earlier in September (Fig. 5.3a). We therefore feel that only assessing movement in September gives a reasonable overview of how the birds move in a novel environment. We only included birds that had completed all 12 trials in the spatial task and for which we had obtained daytime localisations for at least 6 hours/day for a minimum of seven days in September. This dataset comprised 50 individuals (25 female, 25 male) (total 114,067 locations, mean ± SD per individual = 2281.34 ± 774.03) with which to perform the analysis.

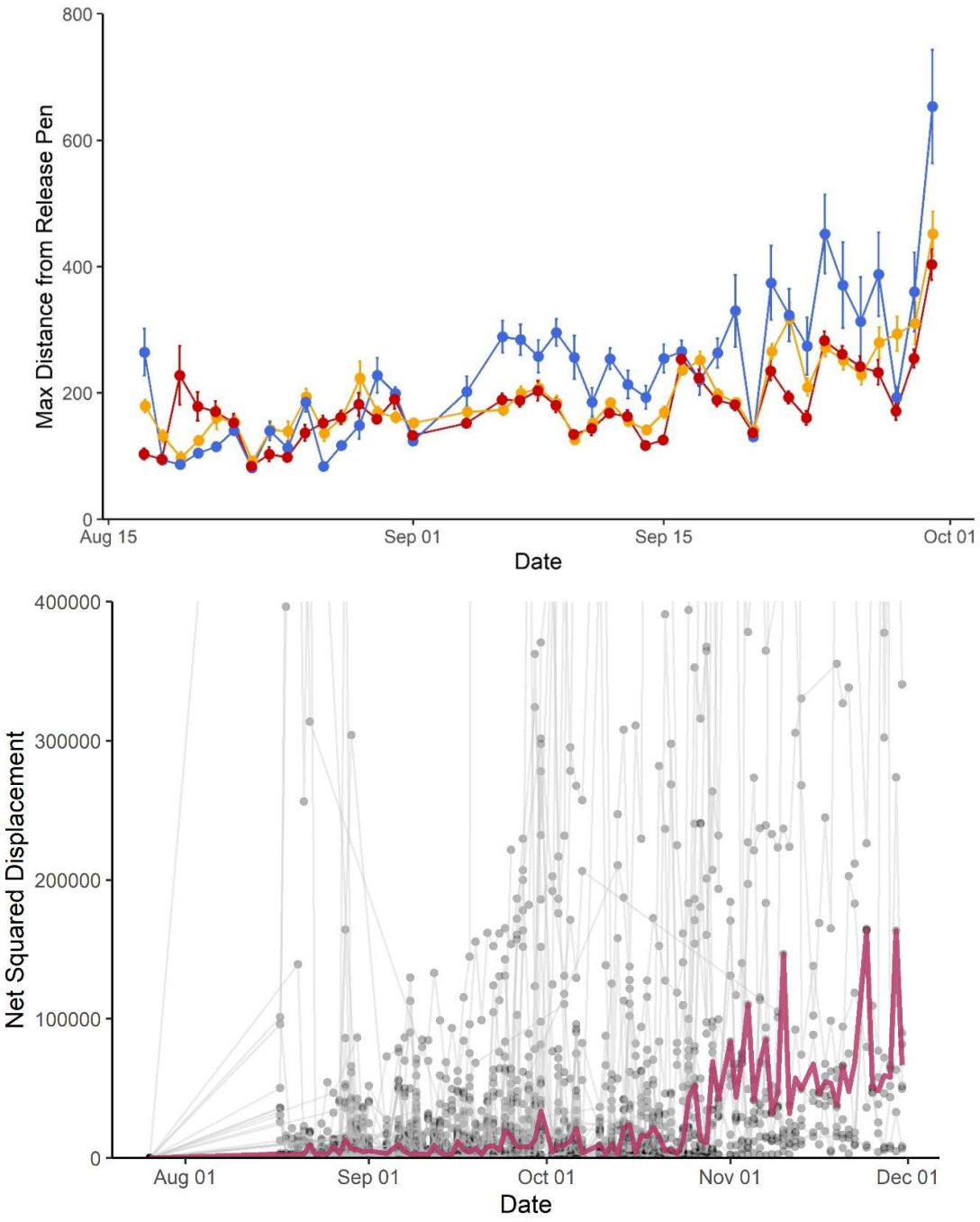


Figure 5.3 a) Daily travel distances of pheasants (mean maximum distance from the centre of the release pen) per day from start of tracking period (15th August) – end of study period (1st October). Error bars are 95 % confidence intervals. Colour indicates performance on spatial task (High (≥4) = blue, Medium (2 or 3)= yellow, Low (≤1)= red) b) Net square displacement from the centre of the release pen from release date to December. Grey circles are mean square displacement (MSD) per day per individual and lines connect points on an individual level. Pink line is the median of the daily MSD for the whole population, demonstrating that dispersal at a population level is around November, although many individuals are exploring outside the release pen from September. There are also 4 individuals that explore far from the release pen (> 500m) before September.

5.3.5 Behavioural classification

We separated each individual's movement paths into different behavioural classes to separate transit from other behaviours, such as resting or foraging. We used a hidden Markov model from the package *moveHMM* v1.6 (Michelot et al., 2016) on ATLAS data to cluster bouts of similar patterns of movement together. Pheasants are diurnal, therefore we only used tracks from between civil dawn and civil dusk (calculated using the *crepuscule* function from the *maptools* package v 0.9-5 (Bivand & Lewin-Koh, 2019)). We split tracks with more than a one-hour window of missing points for each individual. This was to avoid using interpolation to simulate locations in the missing period which, since pheasants often move slowly, can lead to misclassification of tracks as a result of many short steps in a straight line being created. We ran 25 randomisations of the initial parameters for a 3-state model to assess model sensitivity and obtain the model with the best Least-Likelihood Ratio (Grecian, Lane, Michelot, Wade, & Hamer, 2018). Since some step lengths were of length zero, we also estimated zero-inflation within the model (Michelot et al., 2016). We used a Gamma distribution to describe step length and a von Mises distribution for turning angles. The best model separated behaviours primarily by step length (Fig. 5.4). Inspection of the movements of individuals informed us of how we should describe each state, although it should be noted that these are inferred (Fig. 5.5).

State 1, which we determined was most likely to be resting behaviour, was rare during the day and characterised by essentially no movement (Step length (mean ± SD) = 3.581 m ± 2.652 SD; overall displacement: 8.277 m ± 6.302 SD; n = 1027). State 2 involved much longer mean step length and displacement distance (Step length (mean ± SD) = 30.646 m ± 23.758 SD; overall displacement: 96.070

m ± 76.507 SD; n = 1078) and we deemed this to be transit. State 3 was characterised by an intermediates step length and displacement distance (Step length (mean ± SD): 13.855 ± 9.578; overall displacement: 50.130 m ± 37.952; n = 2157) and frequently occurred in the vicinity of feeding stations (Fig 5.5), so we called this foraging behaviour. All turning angles were centred around π although to a lesser degree in transit behaviour, we expect that this is due to slow movement speeds as well as pheasants moving around obstacles. We used the Viterbi algorithm (v*iterbi* function in moveHMM) to estimate the most likely sequence of state changes for each trajectory based on the best fitted model and isolated the sections of the trajectories that were determined to be 'transit'.

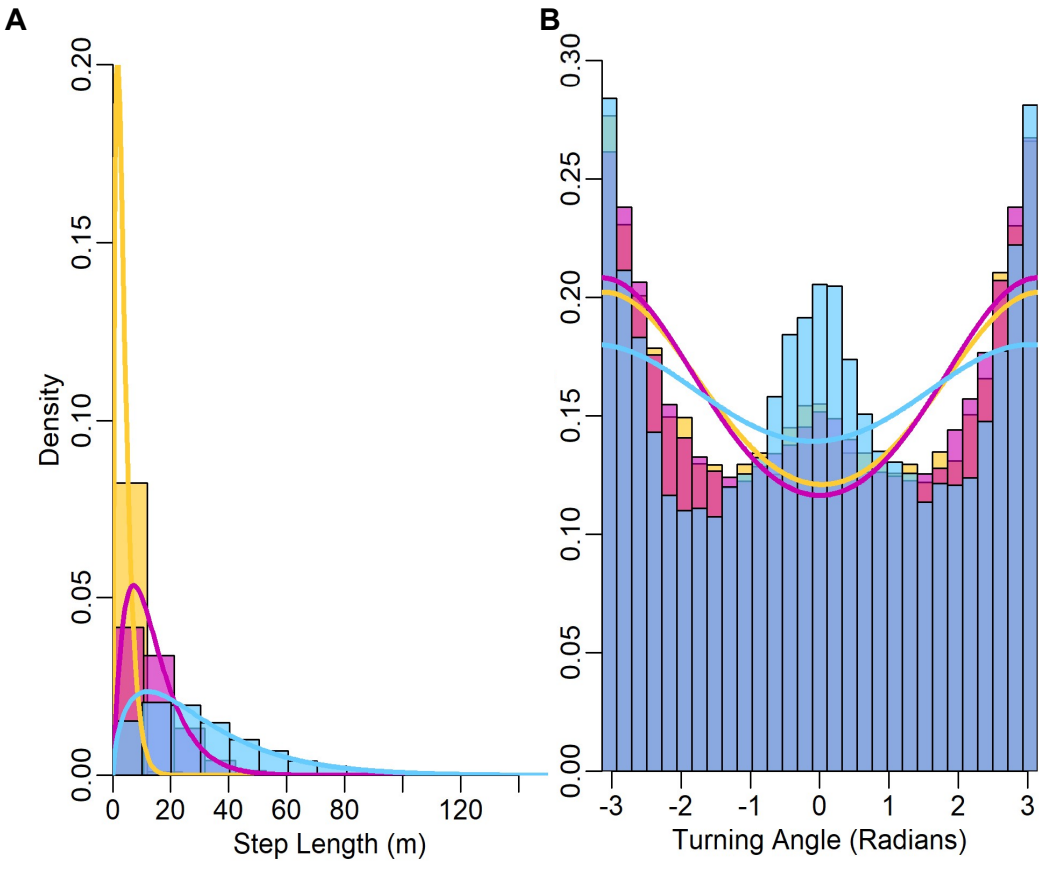


Figure 5.4 Density plots for fitted distributions of a) step length and b) turning angles for each predicted behavioural state. States are overlaid and may appear lighter or darker in areas: State 1 (Resting) = yellow; State 2 (Transit) = blue; State 3 (Foraging) = pink.

5.3.6 Assessing search efficiency

We only considered movement during transit (State 2) to be indicative of demands on efficiency. The mean transit path was about 100m (96.070 m ± 76.507 SD; n = 1078) and usually interspersed foraging bouts, indicating that the focal bird was moving in unprofitable land between profitable foraging patches. It is this movement between foraging sites that could be made more efficient with experience. We consider more efficient paths to be straighter and faster to travel. The time that an individual takes to move between two distant points is likely

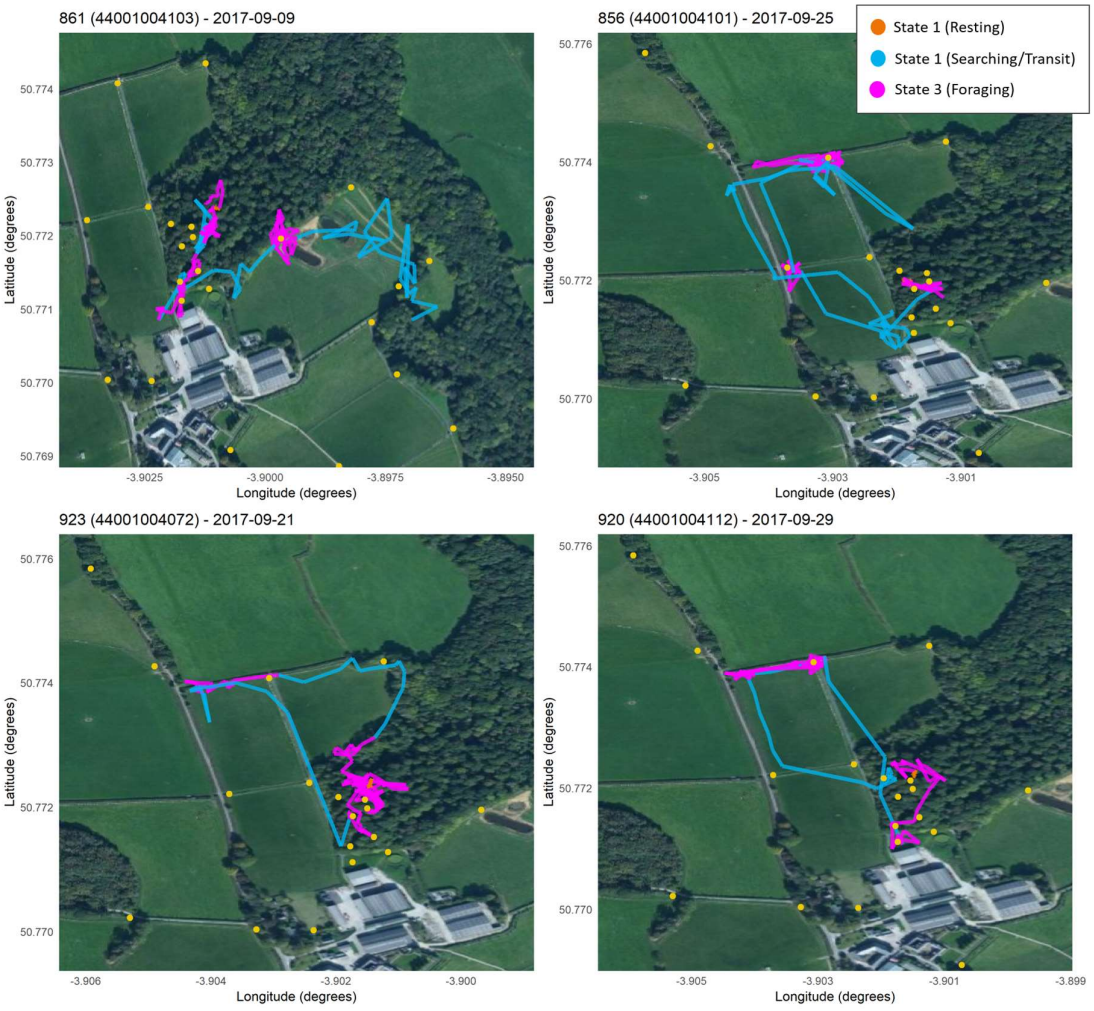


Figure 5.5 Examples behavioural state prediction from moveHMM. State 1 (resting, NB this is minimal): orange; State 2 (transit): blue, State 3 (foraging): pink, yellow circles denote supplementary feeder stations.

determined by their ability to select terrain that is easier to traverse, for instance flat ground or roads. Considering both straightness (distance/path length) and speed (m/s), therefore informs us of movement efficiency through both turn frequency and the relative ease of the terrain. We isolated each section of all tracks that were assigned as transit (State 2) and assessed both straightness and speed using the *amt* package (Signer, Fieberg, & Avgar, 2019). The *straightness* function was used to calculate straightness and we calculated speed by measuring total distance travelled (*tot_dist* function) divided by total time duration in seconds.

5.3.7 Statistical analyses

All analysis was performed in R (v.3.5.3) (R Core Team, 2019) using the R Studio wrapper (v.1.2.1335) (RStudio Team, 2018). All continuous variables were centred and scaled using the *scale* function in R before analysis. We assessed whether pheasants improved their performance on the spatial task using a generalized linear mixed model (GLMM) with a Poisson error structure and log link function. We fitted the number of errors as the response variable with trial number, test order and sex as fixed factors and bird identity as a random effect.

To identify whether any cognitive or non-cognitive traits influenced the speed or straightness of transit paths, we performed a GLMM with a Gamma error structure and a log link function. We included a two-way interaction between date (as a scaled integer) and spatial cognitive ability as well as sex and scaled test order as fixed effects in the full model. Bird identity was included as a random effect in the model and in the straightness model we also included the number of

sampling points used as a random effect to account for differences in straightness between short and long duration tracks. We reduced the model using stepwise model simplification and choosing sequential models with the lowest AIC values, calculated from a likelihood-ratio test (base R function: *drop1*, test = Chi).

We used spatial cognitive ability as a continuous variable in our statistical models. However, for graphical interpretation of any significant interactions we grouped spatial cognitive ability into low (≤1), medium (2-3) and high (≥4) performance groups (where the parameter estimate of the high performance group was most similar to the estimate in the continuous model), reran the final model with these values then used *sjPlot* to plot the model predictions from the GLMM. While we attempted to include a plot using a model with an unscaled date variable (again, to make the model output more easily interpretable), the model would not converge and therefore this could not be used.

5.3.8 Ethical considerations

Handling of all pheasants during rearing and testing was kept to a minimum. Task participation was voluntary and only positive reinforcement was used. Birds were habituated to experimenters and the testing chamber from their first week of life to help alleviate stress that testing procedures may cause. Chicks were kept in less densely populated conditions than is recommended by DEFRA's code of practise (DEFRA, 2010). When capturing wild adults, traps were checked at least three times per day. All work was conducted under Home Office license PPL 30/3204 and approved by the University of Exeter Animal Welfare Ethical Review Board.

5.4 Results

5.4.1 Did birds learn the spatial task?

The number of errors birds made on the spatial task decreased as trial number increased (β ± SE = -0.290 ± 0.037, n = 50, χ^2 = 63.146, p < 0.001). Median test order (β = -0.044 ± 0.075, n= 50, χ^2 = 0.339, p = 0.561) and sex (β = -0.158 ± 0.115, n = 50, χ^2 = 1.162, p = 0.281) had no effect on the performance of individuals in this task. Birds varied in performance score (maximum number of consecutive no error trials) from a minimum of 0 to a maximum score of 9 (Fig. 5.6).

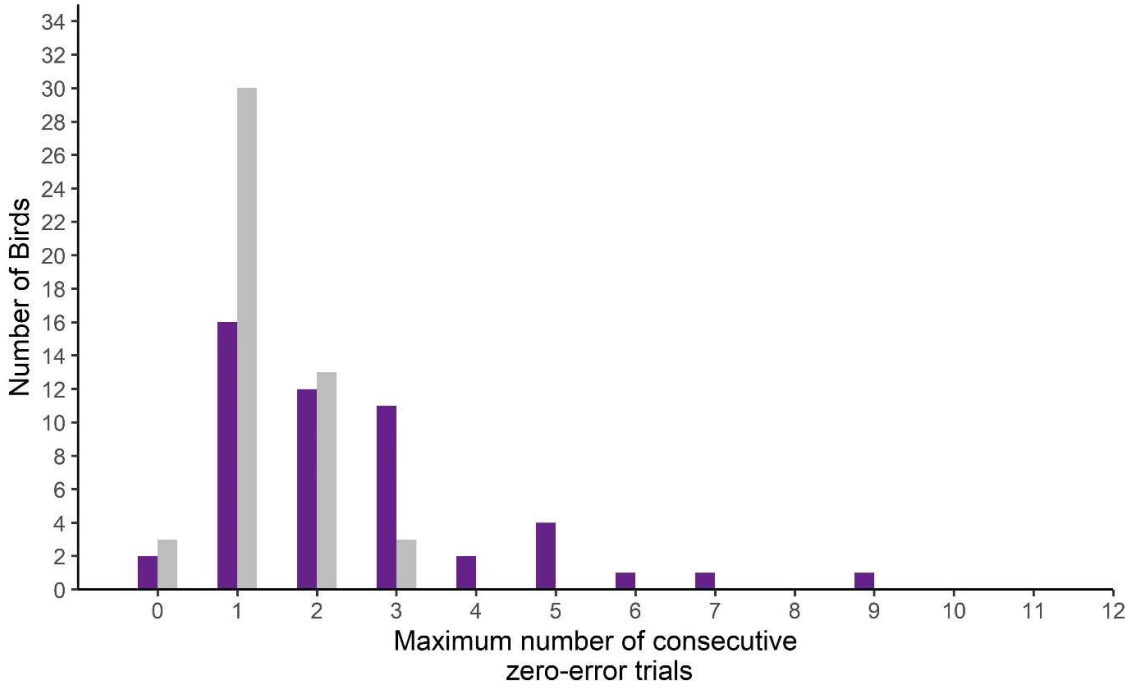


Figure 5.6 Distribution of spatial scores of pheasants (purple) and simulated data (grey).

5.4.2 Does spatial cognitive ability, sex or motivation affect transit efficiency?

Individuals that had high performance scores in the spatial task improved the speed of their transitory paths more rapidly over the month than poor learners,

indicated by a significant interaction between date and accuracy score (Table 5.1). However, more accurate birds also started with slower paths and improved over time to the same level as poor performers (Fig. 5.7). While all individuals increased the straightness of their paths over the study period, there was no difference in the rate of this improvement according to spatial cognitive ability. We also found no differences in overall movement efficiency based on an individual's sex or motivation (Table 5.1).

Table 5.1 Model outputs from generalized linear mixed model of the effects of performance in the spatial task on the speed and straightness of transitory paths. P values and likelihood ratio test values are given when they were removed from the full model, denoted by superscript. * denotes the terms are present in the full model.

Parameter	β ± SE	LRT	p
Speed			
Sex (M)[1]	-0.050 ± 0.074	0.482	0.488
Test Order[2]	0.051 ± 0.035	2.059	0.151
Date*	0.045 ± 0.050	-	-
Accuracy*	-0.014 ± 0.019	-	-
Date x Accuracy*	0.034 ± 0.016	3.707	**0.034**
Straightness			
Date x Accuracy[1]	-0.008 ± 0.012	0.427	0.514
Test Order[2]	-0.006 ± 0.039	0.025	0.875
Accuracy[3]	0.008 ± 0.020	0.160	0.689
Sex[4]	-0.042 ± 0.072	0.333	0.564
Date*	0.100 ± 0.023	19.455	**< 0.001**

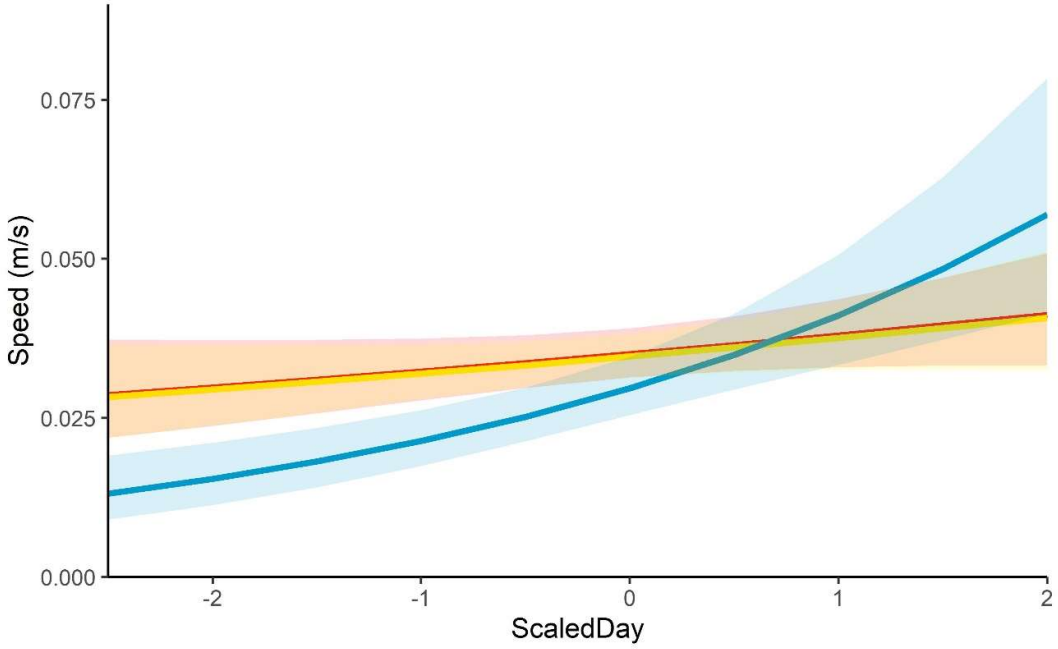


Figure 5.8 Predicted values of straightness (A) and speed (B) over the month of September for individuals exhibiting low performance (0-1; red), medium performance (2-3; yellow) or high performance (>3; blue) on the spatial task. Date ranges from 1st – 30th September (scaled integer value). Shaded areas represent 95% confidence intervals.

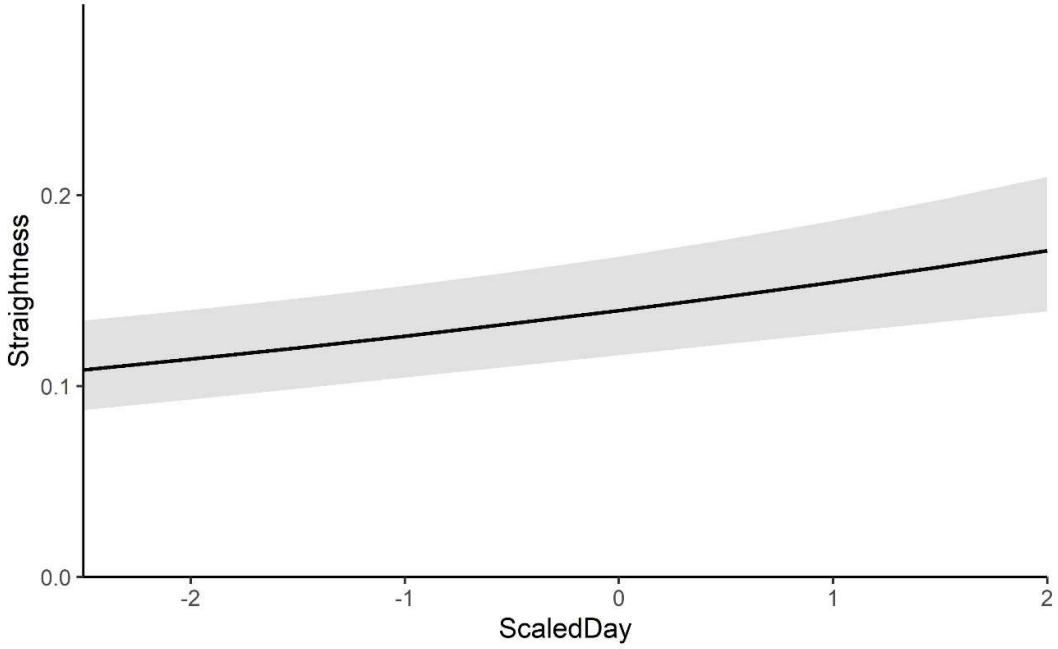


Figure 5.7 Predicted values of straightness over the month of September. Date ranges from 1st – 30th September (scaled integer value). Shaded areas represent 95% confidence intervals.

5.5 Discussion

At the population level, pheasant chicks were able to learn a spatial cognitive task indicative of their referential spatial memory but performance in the task varied across individuals. Performance on the task in captivity predicted their rate of improvement in movement efficiency two months later after they had been released into a novel, real-world landscapes. Specifically, individuals that performed better on a five-arm radial maze initially moved more slowly between areas of interest than their 'poor' performing counterparts at the beginning of the study period. Over a period of one month, these high-performing birds increased their speed to a similar level as individuals of 'poor' spatial cognitive ability who seemed to retain a relatively constant speed of movement throughout the month. While we found that pheasants increase the straightness of their transitory paths in general, this did not differ according to spatial cognitive ability. Nevertheless, this study provides the first empirical insight into the relationship between individual differences in spatial cognitive ability and the development of transitory paths in free-roaming animals.

The speed and straightness of an animal's transitory movements have previously been shown to increase with experience in a particular environment (Carter et al., 2019; Osborne et al., 2013). We expected that individuals may differ in their rates of improvement, according to differences in their cognitive abilities, as measured through cognitive tasks (Boogert et al., 2018; Thornton, Isden, & Madden, 2014), with individuals that performed well (high accuracy birds) in spatial tasks improving at a faster rate than those who performed poorly (low accuracy birds). High accuracy birds started the study period by moving more slowly than low

accuracy birds but by the end of September this difference was no longer apparent. We had expected differences in speed to occur later in the study period rather than at the beginning. This is because we had assumed that an increase in speed would be a consequence of learning quicker routes or simply moving faster as confidence in the route increased with experience. In random search processes, speed, turning patterns and perception govern the success of encounters with resources (Bartumeus et al., 2016), therefore the slower movement by high accuracy birds during the early occupation of a novel landscape may serve to facilitate information gathering in a novel environment.

Speed-accuracy trade-offs are an important consideration for animals (Chittka, Skorupski, & Raine, 2009). Sih and Del Giudice (2012) suggest that slow exploring animals may sacrifice short term gains to make accurate and perhaps safer choices, but this may pay off in the long-term through more efficient foraging and/or reduced risk of predation. Slow-exploring individuals have been shown to sample previously rewarded locations more frequently in great tits, *Parus major* (van Overveld & Matthysen, 2013) and have higher accuracy in cognitive tests in black-capped chickadees, *Poecile atricapillus* (Guillette, Hahn, Hoeschele, Przyslupski, & Sturdy, 2015) than their faster counterparts. Error costs of visiting the wrong places can be substantial and can lead to animals taking longer to make decisions. For example, bumblebees, *Bombus terrestris dalmatinus*, under predation risk move slower and scan flowers for longer, reducing their likelihood of an erroneous choice (Ings & Chittka, 2008). However, within populations of either high or low predation risk, wild guppies *Poecilia reticulata*, show consistency within individuals for ‘hasty’ and inaccurate choices or ‘careful’ and accurate decision making (Burns & Rodd, 2008). It is possible that high accuracy

birds could have used similar tactics to complete the spatial task and spent longer periods of time making decisions than birds that performed poorly. However, we did not measure the time taken for individuals to make their first choice in our tests and therefore cannot detect these differences.

Exploration and cognitive traits have been suggested to be closely linked because slow exploration allows for more accurate information gathering by exhibiting stronger area restricted search strategies, resulting in slower and/or more tortuous trajectories (Sih & Del Giudice, 2012; Spiegel et al., 2017). However, other personality traits such as boldness could also influence the movement patterns of individuals. Bolder individuals are generally defined as more willing to take risks and standard novel-object tasks have been found to correlate with risk-taking strategies in foraging behaviour (Dammhahn & Almeling, 2012). Boldness has been demonstrated to be linked to dispersal tendencies and metabolic rate in gobies *Neogobius melanostomus* (Myles-Gonzalez, Burness, Yavno, Rooke, & Fox, 2015) and bolder bank voles *Myodes glareolus,* have larger home ranges containing different microhabitats and travel further than shy voles (Schirmer, Herde, Eccard, & Dammhahn, 2019). Routes to resources may differ in habitat type and the straightest or fastest route may be a 'riskier' route. We may therefore expect that bolder individuals may be more willing to take straighter routes if there is a difference in risk. Future research should attempt to incorporate measures of personality within a battery of tasks.

After 52 days in the environment, high accuracy birds had increased their speed of transit from slow movements to at least the speed of low accuracy birds in the

novel landscape. Further research would be useful to identify whether this improvement continues for the birds that performed well in the spatial task in the subsequent months (as is indicated by the trajectory of the model prediction in figure 5.7), resulting in higher overall efficiency and attendant fitness benefits. The differences in movement speed over time that we observed could not be explained by differential opportunities to learn between individuals because all birds were naïve to the environment and, being released on the same day at the same site, had equal experience of it. In addition, the change in speed, or lack of change in the case of low and medium accuracy birds, is unlikely to be explained by differential access to informed individuals. We had removed all parents from the study site and did not detect them on the site again during our tracking period. Although there is the possibility of our test birds following wild, experienced non-parent adults that we did not capture or detect, all our released birds had equal access to them, being released at the same time and in the same place.

In accordance with other studies (Carter et al., 2019; Osborne et al., 2013), we found that pheasants increase the straightness of their transitory path as they gain experience of an environment. However, in contrast to our predictions we found no difference between individuals of differing spatial cognitive ability in the straightness of their transitory paths. The lack of relationship between spatial cognitive ability and straightness of transitory paths could have several explanations. First, in species where transit can often occur with direct routes and few obstacles, straightness is an obvious and informative measure of efficiency since turning is costly (Wilson et al., 2013). In the case of a terrestrial bird in a rural landscape, many obstacles and varying terrain could obscure the most 'efficient' path with respect to straightness, but this should be relative between

individuals released into the same area. However, this measure is further complicated by the differences in start and end points of transitory paths both between and within individuals over different days. Investigations into the variability of track end points may indicate whether spatial cognitive ability is linked to the ability to travel to specific locations consistently. However, birds may vary in the number of locations they attempt to visit and determining the goal of an animal's trajectory in the wild is not a trivial task. Furthermore, foraging strategy or diet choice may differ between individuals, potentially leading to differences in movement strategies (Bergmüller & Taborsky, 2007; Patrick et al., 2014; Whiteside et al., 2015). Despite knowing the specific locations of high value feeders, we did not know the locations of all resource patches and prey such as insects may be particularly variable. Other factors such as predator risk and social factors are also highly unpredictable and could influence also the end point of a transitory path (Hintz & Lonzarich, 2018; Liesenjohann & Eccard, 2008; Metcalfe, Huntingford, & Thorpe, 1987).

We acknowledge that we were unable to track each individual from their release date due to technical difficulties, however we demonstrated that the birds typically began to explore beyond the pen in September and were therefore likely to have remained in the close vicinity of the release area prior to the tracking period. One relatively subtle difference between birds of differing performances is that more accurate birds began exploring outside the release area sooner (the beginning of September) than poor performers (mid-September). This may drive slower movements for information gathering exploration in the more accurate birds at the start of September, after which it is possible that low accuracy birds could

utilise social information to retain the efficiency that they display around the release area (Langley, van Horik, et al., 2020).

We found no effects of sex on performance on the spatial task or movement efficiency in our study. Previous research has found distinct sex differences in spatial cognitive ability in the form of larger home ranges (Gaulin, FitzGerald, & Wartell, 1990), more complex habitats (Lucon-Xiccato & Bisazza, 2017) or differential breeding biology (Guigueno et al., 2015). Pheasants display pronounced sexual segregation in association behaviour from November until February (Whiteside et al., 2019) and females typically disperse further than males (Hill & Ridley 1987). It is therefore surprising that we did not find differences between the sexes in spatial cognitive ability and/or movement efficiency. However, this may be due to the short study period which occurred early in the bird's life and annual cycle: before sexual segregation and the opportunity to disperse far.

The suggested relationship between spatial cognition and movement, presumed to be key to efficient space use (Fagan et al., 2013; Nathan et al., 2008) has lacked empirical support. We have utilised the widely accepted method of measuring performances on an abstract cognitive task to provide a useful assay of inter-individual variation in spatial cognitive ability (Boogert et al., 2018; Thornton & Lukas, 2012) and asked whether this links to changes in movement behaviour, specifically changes in path efficiency over time in naturalistic, real-world landscapes. While we did not find links between spatial cognitive ability and changes in path straightness, we did find that the change in speed of transitory

routes differs between individuals according to their spatial cognitive ability. Our study demonstrates a subtle link between the inherent ability of an individual to collect, process and utilise spatial cues in a controlled environment, measured early in life having been reared under identical conditions, and the development of a movement strategy later in life when in a complex natural landscape. This provides a crucial, empirical link between spatial cognitive ability and movement ecology.

6 Individual orientation strategies shape habitat preferences in the wild

6.1 Abstract

Cognitive representations of the spatial environment have been suggested to be encoded in one of two systems. Individuals can orient either in relation to themselves (egocentric) or other environmental features (allocentric) and each strategy can be used independently or in conjunction with one another. The strategy exhibited by particular populations or species may relate to the habitat type that they currently occupy. However, an individual may preferentially occupy these particular habitats because they find them easier to navigate by using orientation strategies established early in their life. We asked whether attention to either egocentric or allocentric cues while learning a maze task when young and reared under controlled conditions explained individual differences in habitat selection in the wild later in life. First, we trained pheasant chicks, *Phasianus colchicus,* on a dual-strategy maze task before rotating the maze so that allocentric, not egocentric cues would indicate the correct route. We found that 47 % of individuals relied heavily on allocentric cues, whereas the other birds relied at least partially on egocentric cues to learn the maze. After testing, birds were released, and subsequent habitat selection was continuously monitored using a reverse GPS system. Individuals that used an egocentric strategy in the maze task, thus not using landmarks, were less likely to use areas containing conspicuous human artefacts (buildings, roads, yards etc). We found no differences in use of woodland or open habitat. This suggests that orientation strategies determined early in life may influence the habitats that an individual preferentially occupies, with those that rely on landscape features choosing to inhabit areas where such distinct landmarks are prolific.

6.2 Introduction

Many animals utilise information about their environment to efficiently navigate between places of refuge and resources and so reduce energetic costs and risk. They may achieve this by encoding spatial information using one of two spatial reference systems (Burgess, 2006; O'Keefe & Nadel, 1978). Firstly, locations can be construed relative to the observer, known as egocentric or route learning. This can constitute directional responses, such as a sequence of turns or by monitoring the distance and direction travelled facilitating path integration (Huber & Knaden, 2015). Alternatively, spatial information may be encoded independent of observer position, and instead relative to the position of environmental features such as landmarks. This is termed allocentric or place learning and allows an individual to navigate to a target location from any direction utilising stable environmental cues (Normand & Boesch, 2009). There is evidence that these two strategies are neurologically independent of one another in mammals (Aagten-Murphy & Bays, 2019; McDonald & White, 1994), birds (Fremouw et al., 1997; Shimizu et al., 2004) and fish (Broglio et al., 2003; López et al., 1999), although both strategies can be used in parallel to navigate effectively (Rodriguez, Duran, Vargas, Torres, & Salas, 1994). Preferential utilisation of particular orientation strategies may vary with task type or the salience of cues (Cole, Clipperton, & Walt, 2007; Dudchenko, 2001) but there may also be distinct individual differences as demonstrated in humans (Marchette et al., 2011) and cuttlefish *Sepia officinalis* (Alves, Chichery, Boal, & Dickel, 2007)).

Differences in orientation strategy may arise because of the habitat that an individual occupies, probably because habitat structure determines the salience

of cues used in navigation. Across species, mound-building mice *Mus spicilegus*, outperformed eastern house mice *Mus musculus musculus*, on an egocentric-only maze task, presumably because the former relies solely on egocentric cues to navigate its burrows in winter, whereas the house mouse can utilise both allocentric and egocentric strategies by living in a more open habitat year-round (Bruck, Allen, Brass, Horn, & Campbell, 2017). Within species, three-spined sticklebacks, *Gasterosteus aculeatus*, from fast-flowing river habitats, where turbulent waters may make landmarks ineffective predictors of location, orientate primarily using an egocentric strategy (Odling-Smee & Braithwaite, 2003). In contrast, sticklebacks taken from stable pond environments rely more heavily on allocentric cues. While individuals taken from populations in differing habitats exhibit distinct orientation strategies; within a population, habitat preference can vary at the individual level (Leclerc et al., 2016). If individuals are more inclined to use one strategy over the other, as in humans (Ferguson, Livingstone-Lee, & Skelton, 2019; Marchette et al., 2011), habitat selection may be a consequence of a pre-disposition to use one cue type. To investigate the possibility that habitat selection may be either a cause or consequence of a 'preferred' or inherent orientation strategy, strategy use should be assayed under controlled conditions before observing an individual's pattern of habitat occupation. This is not trivial for two reasons. First, it is hard to assay numerous naïve individuals for their orientation strategy under controlled conditions and then release them into the wild. Second, it is difficult to continuously track those individuals from their arrival in the wild at sufficiently high spatial and temporal resolution that accurate measures of habitat preference can be obtained.

Mazes, typically where the goal location is baited with food or provides an escape, are frequently used to assay orientation strategies (Grech, Nakamura, & Hill, 2018). The type of cues used to successfully complete the maze can be assessed in one of two ways. Firstly, single-strategy mazes, where either stable allocentric or egocentric cues are provided, but not both, provide an effective assessment of proficiency with a particular strategy (Bruck et al., 2017; Rodriguez et al., 1994). Secondly, dual-strategy mazes (with consistent egocentric and allocentric cues) allow an animal to learn to navigate a maze with either cue type. After the learning phase, the orientation strategy used can be assessed with a single-strategy probe trial, whereby good performance suggests that the animal used the same strategy to learn the task and poor performance suggests attention to the other cue type or a combination of both (Alves et al., 2007; Ferguson et al., 2019; Tierney & Andrews, 2013).

Pheasants, *Phasianus colchicus*, provide a useful system with which to investigate links between orientation strategies and spatial ecology. Chicks can be reared under controlled conditions in large numbers from hatching, accounting for potential effects of experience in habitat variation or maternal influence on any assays of cognitive processes. Furthermore, individual differences in their spatial cognition are well documented (Langley, van Horik, Whiteside, Beardsworth, et al., 2018; Langley, van Horik, Whiteside, & Madden, 2018b; Whiteside, Sage, et al., 2016) although individual differences in orientation strategy use have so far been ignored. In the UK, juvenile pheasants are released into the wild to supplement hunting stock on an annual basis. This provides a unique opportunity to measure the cognitive abilities of young individuals that have been reared under controlled, captive conditions before releasing birds and monitoring their

behaviour as free-roaming individuals. In the wild, pheasants utilise a range of habitat types, including complex and cluttered woodland environments, open farmland and rural agricultural yards and buildings. Habitat use differs by sex with females feeding more often in woodland than males (Hill & Ridley, 1987), so we may also expect to detect sex differences in orientation strategy.

Consequently, we can assess an individual's strategy use early in life, with chicks having been reared under identical conditions and tested using a standardised maze task. We can then observe patterns of habitat preference after their release into the wild. We expect that individuals will differ in their later habitat preferences according to the orientation strategy that they used early in life. For animals using an allocentric strategy, we expect that they will prefer habitats where landmarks are conspicuous, distinct and consistent. Such habitats may be relatively open and contain distal landmarks such as unique horizons, geographical features or anthropogenic structures. In contrast, for animals using a primarily egocentric strategy, we expect that they will occupy habitats where distal landmarks are absent or obscured. Such habitats may contain short fields of view such as found in woodlands or dense foliage such as standing crops. In this study, we explored which cue types (allocentric or egocentric) pheasants used to solve a complex maze task, and whether individuals differed in their strategy, despite homogeneity of rearing environment. We then monitored the same pheasants in the wild and assessed their use of open, urban and woodland habitats to investigate whether individual differences in orientation strategies influence habitat preference in free-roaming birds.

6.3 Methods

6.3.1 Subjects and Housing

One hundred and twenty-six pheasant chicks were habituated to human experimenters from one day old (24th May 2018) and housed in four groups (3 x n=32, 1 x n= 29) with *ad libitum* access to age appropriate food (Keeper's Choice, Norfolk, UK) and water. They were shaped to voluntarily enter a 75 cm x 75 cm testing chamber using positive reinforcement (mealworm rewards) during their first 3 weeks of life. Birds entered the testing chamber from their holding pen (1 m x 2 m) through a sliding door and exited through a pulley-assisted door to a separate pen (0.75 m x 1.25 m) with further access to an unheated outdoor shelter (1.5 m x 2.4 m) and an outdoor enclosure (4 m x 12 m). All birds were individually identifiable using numbered patagial wing tags.

6.3.2 Maze Task

At 5 weeks old (3rd – 5th July 2018), the testing chamber was segmented into a 3 x 3 cell maze using 35 cm high walls of opaque black plastic (Fig. 6.1). Birds were habituated to the maze using mealworm rewards scattered throughout the cells, with all walls between cells having 10 cm wide openings giving access to all neighbouring cells. Once birds were voluntarily entering the chamber alone with no obvious signs of stress, we added 4 extra walls and closed off access to the exit cell from 2 of 3 neighbouring cells. This created a maze structure which required a minimum of 7 orientation decisions to efficiently negotiate to the exit cell where they attained 3 mealworms and could exit the maze (Fig 6.1). We assessed performance in the maze by counting the number of cells a bird entered

(defined by the bird's head entering a cell) and subtracting 7 (the minimum possible choices) from the total.

Birds completed eight training trials to permit learning about the maze. Extra-maze (allocentric) cues such as the experimenter's location or the pulley system for the exit door (which ran in a straight line from the experimenter to the opposite wall of the testing chamber) were the same across pens and could be used as an alternative to, or in addition to the route-learning of an egocentric orientation strategy. After the eighth training trial, birds in two of the pens were swapped to pens where the maze had undergone a 180-degree rotation (Fig. 6.1) so that egocentric cues, but not allocentric cues were disrupted. As a control, birds in the other two enclosures were moved to pens that had an identical maze oriented in the same way as in their previous pen and surrounded by the same extra-maze cues so birds could continue to use the same strategy whether egocentric or allocentric to complete the maze.

The birds were then left overnight to habituate to their new pen although separated from the novel mazes. The following day (6th July 2018), the chicks were given a probe trial on the maze task in their new pens. In order to determine which orientation strategy an individual was using, we made explicit predictions about how we expected them to move when in the new maze for the first time. In the experimental group, birds that used an egocentric or mixed strategy were expected to attempt to utilise a route that was no longer possible (Figure 6.2 .2). This route was blocked on the first turn therefore we expected them to make more errors (perhaps many more, since the memory of the route is totally disrupted)

and be slower to complete the trial than the control group. Alternatively, if birds were using allocentric cues such as observer location then we expected them to follow the same path relative to those external cues and therefore treatment would have no effect on their number of errors made (Fig. 6.2). Equally, birds that use a combination of both strategies may also make more errors since the

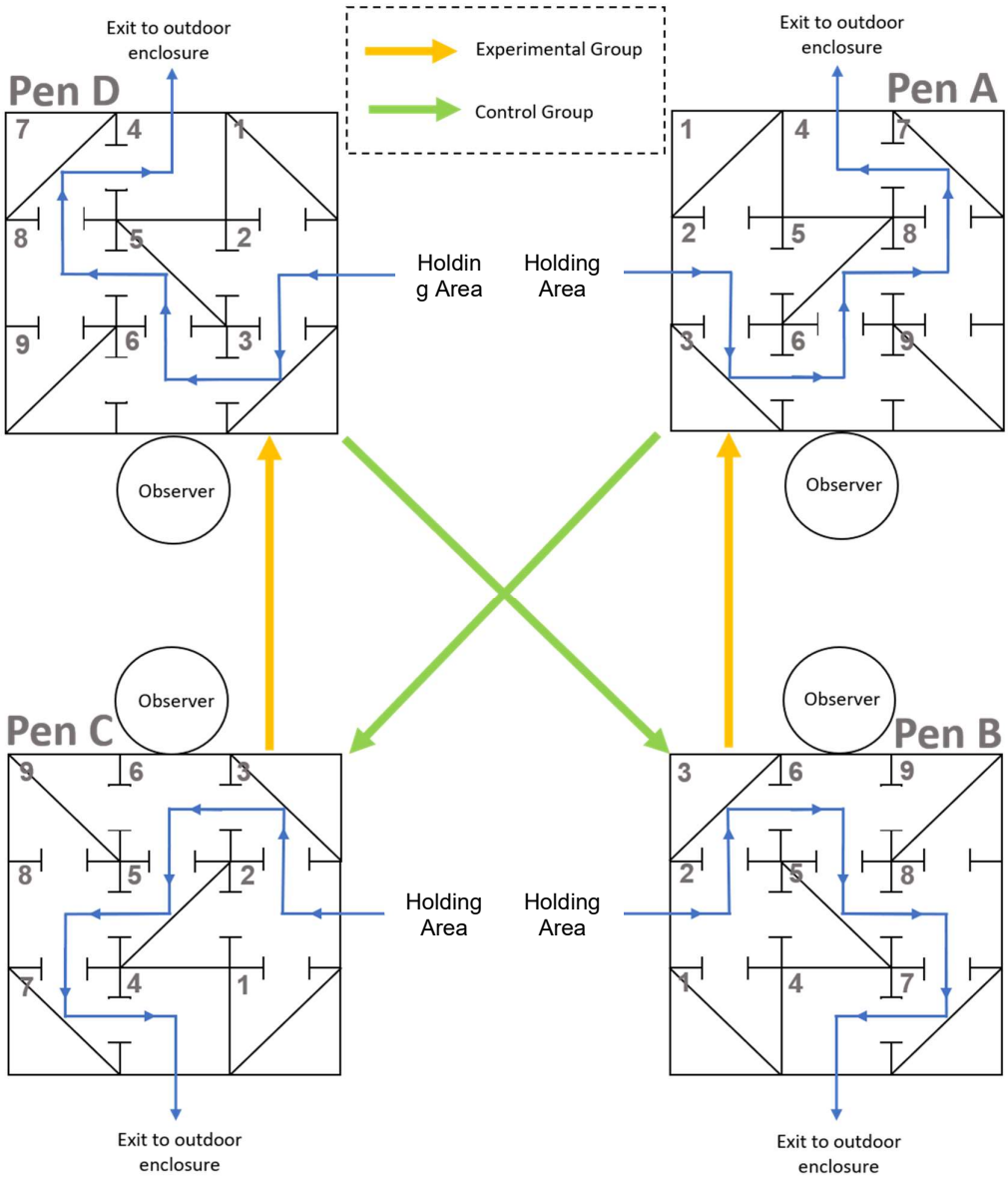


Figure 6.1. Maze task schematic for each pen. Blue line indicates the most efficient route for pheasants to reach rewarded/exit cell (4). Each pen consists of a holding area, maze and outdoor enclosure. For the control group, the route to the reward/exit does not change. For the experimental group, the route is rotated 180° so that if they follow egocentric cues they will make more errors.

disassociation of the cues may cause confusion. In essence, the involvement of egocentric cues in a bird's orientation strategy should lead to more errors overall and we predicted a bimodal distribution in 'improvement' score demonstrating the two different strategies within the experimental group. Seventy-eight birds (control = 24 (F), 20 (M), experimental = 17(F), 17(M)) completed all eight training trials and the probe trial.

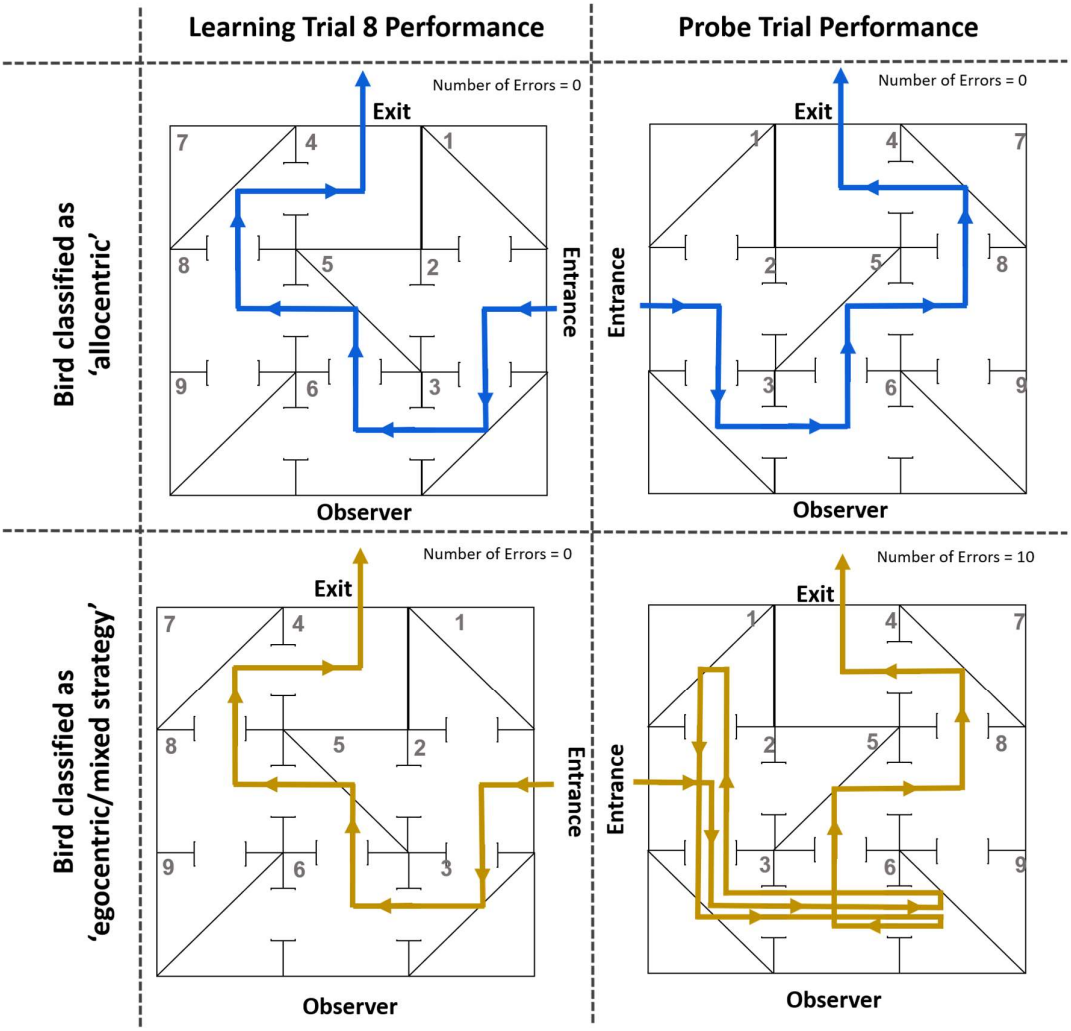


Figure 6.2 Differences in the performance of birds classified as allocentric (no difference or improvement between final learning trial and the probe trial) and egocentric or mixed strategy (more errors in the probe trial than the final learning trial). Here, we show two birds from the experimental group that had zero errors on their final learning trial and were classified as allocentric (top row) and egocentric/mixed strategy (bottom row) based on their response to a rotated maze. The correct route that would be taken by a bird 2, 3, 6, 5, 8, 7, 4.

6.3.3 Release of birds

At nine weeks old, birds were sexed (via plumage) and tagged with ATLAS radio tags (see below). We monitored the birds for one week in captivity to assess tag effects after fitting, before releasing them into an open topped pen ~4000m^2 from which they were protected from terrestrial predators. The pen was situated in woodland on the same farm on which they were reared. Birds could disperse by flying over the top of the fence and could re-enter through one-way tunnels. We provided supplementary food (wheat) at 43 artificial, fixed site feeders situated throughout our field site.

6.3.4 Tracking birds after release

We tracked the birds using a reverse-GPS system (ATLAS) from 26th July 2018 – 10th February 2019. Briefly, this system utilises fixed position receiver stations to detect and collect the time of arrival data from tag-derived radio-signals. These data are then collated at a database on a central server where location is calculated. Location data can be accessed in real-time through an internet connection which allows for continuous monitoring. After smoothing and filtering the data (see Chapter 4 for more details), locations were collected at a resolution of one per 5 mins during the day (from civil dawn to civil dusk) as long as the bird was in range of reception. We only analysed data from birds in the experimental group (n = 34), since only they had a classification for egocentric or allocentric strategy use. To ensure that the locations that we assessed were of live birds, we conducted a detailed search of the field site, using traditional radio tracking techniques guided by the ATLAS system. We confirmed the deaths of 14 (experimental) birds by finding corpses and retrospectively assigned a date of death by manually assessing trajectories of the ATLAS tags until the cessation of

movement occurred. We assessed the trajectories of remaining birds to ensure that all movement included in the analysis was 'natural', indicating that the bird was likely alive with the tag attached. Five birds were removed from the analysis as their trajectories did not appear to be natural movement, we suspect that these tags had been buried but we did not find them. Twenty-nine birds from the experimental group (12 females, 17 males) were suitable for use in the habitat analysis. We used data from the day after release to either the final day of tracking (10th February 2019) or the day before death/tag fell off. This gave us a total of 213,060 locations overall (mean ± SD 7437 ± 6383.351 per individual).

6.3.5 Determining habitat preference of free-living birds

We assessed habitat preference of woodland, open and urban habitats by calculating the time that each individual spent in each area relative to their availability. We used the *National Forest Inventory Woodland GB 2017* shapefile (accessed 21st February 2019: http://data.gov.uk) as a base for our habitat map. Definitions of woodland for the national forest inventory is a minimum area of 0.5 hectares with a minimum width of 20 m unless a narrow corridor connects two or more woodland areas. This did not include most hedgerows, but we felt that hedgerows likely gave similar visibility to open habitat and these were therefore classified as such. We manually digitised urban habitats, classified as farm yards, gardens, buildings and rural homes and gardens using a Bing satellite layer (print rights under the Microsoft ® Bing™ Maps Platform API's Terms of Use, April 2019) for reference in QGIS (QGIS Development Team, 2017). Areas that were not covered by woodland or urban habitats were classified as open habitat. These included grazing ground, unimproved grassland, hedgerows and two small areas

of wetland. The final habitat map covered a 3 km x 3 km area and encompassed all movement of the 29 experimental birds used in this study (Fig. 6.3).

We excluded locations that were situated within the release pen, since the enclosure restricted movement between habitats. Habitat preference was determined by comparing the amount of habitat that was used by an individual to the available habitat (Manly, McDonald, Thomas, McDonald, & Erickson, 2002).

Figure 6.3 Landscape of the study site. Woodland (green), urban (blue) and open landscape (not coloured). The 99 % minimum convex polygon is overlaid to demonstrate the area within which was used to create the random points. All location data from within the area of the release pen (yellow) was excluded. Zoomed area is the main urban environment of the study, the satellite photo demonstrates the type of stable cues that pheasants may use as landmarks.

To determine use, we selected a random sample of 50 % of the total points per individual to minimize autocorrelation (as in Klaassen and Broekhuis 2018). To assess availability of habitat, we generated *n* random points (*spsample* from *sp* package v1.3-1 (Pebesma & Bivand, 2005)) where *n* points produced matched the number of locations of each individual for comparison. Pheasants have very high overlap of range shortly after release, when all movements originate from the release pen. We therefore generated points within the 99 % minimum convex polygon of all individual's 'used' data combined (calculated using *adehabitatHR* v0.4.6 (Calenge, 2006)) rather than generating an available area per individual. We repeated this process 10,000 times and calculated the mean available habitat per individual. Finally, we calculated Manly selection ratios (proportion of habitat used divided by the proportion of habitat available) for each habitat type and individual (Manly et al., 2002).

6.3.6 Statistical Analyses

All statistical analysis was performed in R (v.3.5.3) (R Core Team, 2019) using the R Studio wrapper (v.1.2.1335) (RStudio Team, 2018).

To investigate whether the birds learned the maze task at a population level, we fitted a generalized linear mixed model (*lme4* v1.1-21 (Bates et al., 2015)) with a Poisson error structure and log link function to predict whether number of errors decreased with trial number. We added an interaction between sex and trial number to determine if there was a difference in learning rates between sexes. We also included treatment as a main effect to explore whether any differences in performance on the later probe trail could be due to differences during the

training period for the two groups. Bird ID was included as a random effect. Model reduction was performed by calculating AIC of potential models using the *drop1* function from base R until the minimum model was determined.

We assessed an individual's orientation strategy use by measuring the difference in errors between the final training trial and the probe trial. Individuals in the experimental treatment that maintained or improved performance in the trials after their switch to a new pen were considered to be using an allocentric strategy which remained efficient even in the new pen. In contrast, birds that made more errors after their switch were considered to have used an egocentric strategy to learn the maze. To assess what factors explained individual differences in their orientation strategy, we fitted a binomial GLM where improved performance/allocentric (0) and worsened performance/egocentric (1) learning was used as the response variable. Sex and treatment were included as fixed effects to test whether differences in strategy existed between sexes and to confirm that the control treatment outperformed the experimental treatment. A difference between treatments was expected if some or all learners attended to egocentric cues in the learning phase and no difference was expected if pheasants used allocentric cues. We fitted both sex and treatment as fixed effects, as well as an interaction between them. Finally, we investigated within-treatment differences in improvement score using chi-square tests. This determined two things. First, we confirmed that birds in the control treatment were improving in performance between the final learning trial and probe trial, which was indicative that the birds attempted to solve the original and probe mazes in the same way. Second, for the experimental treatment, we assessed whether one strategy was dominant and expected more birds to 'improve' if they followed

an allocentric strategy and make more errors in the probe trial than in the final learning trial if they followed an egocentric strategy.

To determine preference for habitat types for each individual after release into the wild we fitted generalised linear models with a binomial error structure (used versus available habitat as the response variable) and a logit link function. We fitted three such models, one for each habitat type (open, urban and woodland). We included orientation strategy use in the maze task (egocentric or allocentric) and sex as fixed effects. For each model we first included an interaction term between sex and orientation strategy before performing stepwise model selection using the *drop1* function in base R.

Results

6.3.7 Did the pheasants learn the maze task?

Over the eight training trials, pheasant chicks reduced their number of errors (Trial 1 mean ± SD: 5.09 ± 6.229; Trial 8 mean ± SD: 3.841 ± 5.677) as trial number increased (β± SE = -0.021 ± 0.011, n = 78). Males showed a slightly faster reduction in errors, indicative of faster learning, than females (β± SE = -0.064 ± 0.017, n= 78, LRT = 13.487, p <0.001, Fig. 6.4). There was no difference between the control and experimental birds in their rate of reduction in errors (β± SE = -0.058 ± 0.132, n = 78, LRT = 0.193, p = 0.660).

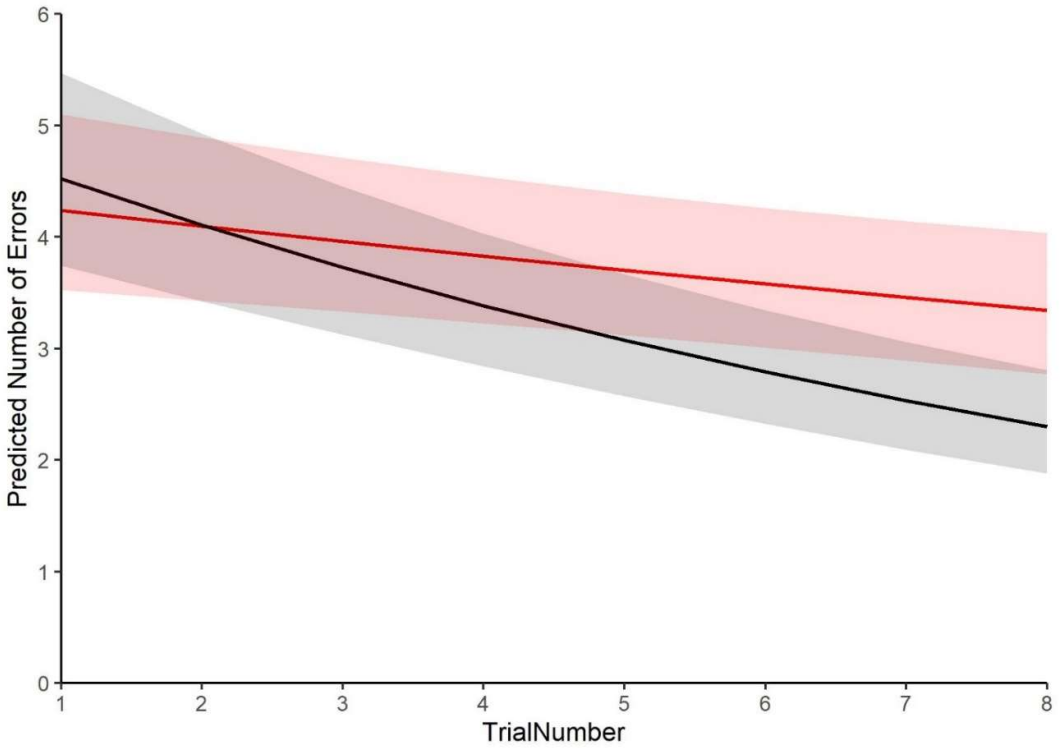


Figure 6.4 Modelled (GLM) rate of learning for males (black) and females (red) over the 8 training trials

6.3.8 Did birds vary in chosen orientation strategy?

Birds in the control treatment continued to improve in their probe trial relative to their final training trial and did more so than birds in the experimental treatment (GLM: β ± SE = 1.783 ± 0.537, n = 78, LRT = 12.277, p <0.001, Fig. 6.5). We found no difference between the sexes in 'improvement' between the final training trial and the probe trial (GLM: sex:treatment: β ± SE = 0.125 ± 1.079, n=78, LRT = 0.013, p=0.908) and sex had no influence on 'improvement' overall (GLM: β ± SE = -0.05 ± 0.537, n = 78, LRT = 0.009, p =0.923).

Within the control treatment, the majority of birds (37/44) improved their performance between the final training trial and the probe trial (χ^2 = 20.455, df =

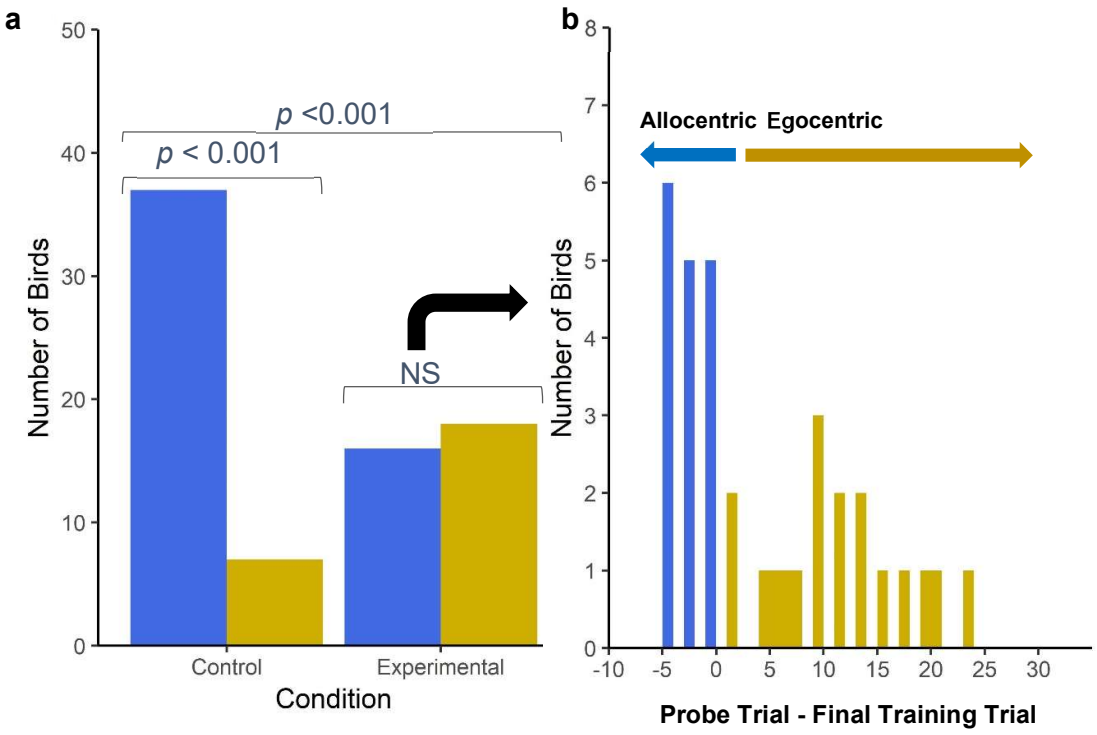


Figure 6.5 a) Bar chart showing the number of birds that made the same or fewer errors on the probe trial (blue) and birds that made more errors on the probe trail (yellow). b) The distribution of the improvement classification (allocentric = blue, egocentric = yellow) in the experimental treatment, with smaller numbers indicating greater improvement.

1, p <0.001, Fig. 6.5a). In contrast, in the experimental treatment there was a similar proportion of birds that showed an improvement between the final learning trial and the probe trial (n = 16) and those that exhibited a worsening of their performances (n = 18) (χ^2 = 0.118, df = 1, p = 0.732, Fig. 6.5a). There was a bimodal distribution of errors of improvement scores indicating two distinct strategies (Fig. 6.5b).

6.3.9 Habitat Preference

Pheasants overall preferred woodland habitat over both open and urban habitat and were present in woodland more than was expected by chance (Fig. 6.6). All pheasants avoided open habitat more than was expected by chance (Fig. 6.6). We found no interaction effects between sex and orientation strategy in any of the habitat types. Male pheasants used more open and urban habitat but less woodland habitat than female pheasants (Table 6.1, Fig. 6.6). Habitat

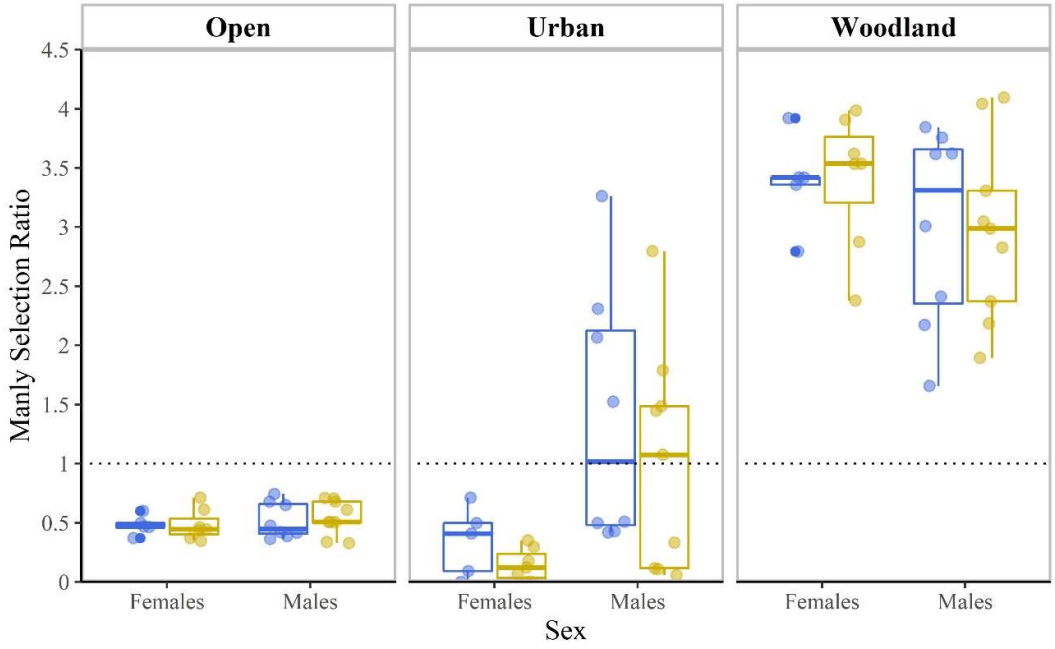


Figure 6.6 Manly selection ratios for birds in each habitat for males and females. Blue = allocentric, yellow = egocentric/mixed strategy. Horizontal line at y = 1 indicates chance level, where no overall preference or avoidance is shown.

preferences also varied according to an individual's orientation strategy assayed in the maze. Birds that used allocentric cues to solve the maze also used the urban environment more than birds that relied on egocentric cues (Fig. 6.6). However, female pheasants, regardless of orientation strategy, strongly avoided urban habitat. In contrast, egocentric/mixed strategy males had no preference but allocentric males held a slight preference for urban habitat.

Table 6.1 Results from binomial generalised linear models (response: used vs available) for 29 birds (12 female, 17 male).

Habitat	Parameter	Estimate ± SE	LRT	P
Woodland	Strategy x Sex[1]	0.018 ± 0.060	0.090	0.764
	Strategy (Egocentric)[2]	0.003 ± 0.028	0.012	0.912
	Sex (Male)*	-0.259 ± 0.030	78.13	< 0.001*
Open	Strategy x Sex[1]	-0.024 ± 0.042	-0.335	0.563
	Strategy (Egocentric)[2]	0.006 ± 0.019	0.098	0.754
	Sex (Male)*	0.187 ± 0.021	82.915	< 0.001*
Urban	Strategy x Sex[1]	0.351 ± 0.220	2.612	0.106
	Strategy (Egocentric)*	-0.341 ± 0.075	21.051	<0.001*
	Sex (Male)*	1.678 ± 0.101	315.260	<0.001*

6.4 Discussion

We demonstrate that individual pheasants differentially use either egocentric and/or allocentric orientation strategies to learn a maze task early in life, and that this strategy, in addition to sex, is linked to their habitat preference in the wild later in life. While males learned the maze task at a faster rate than females the actual difference in error reduction between the sexes was minor. The sexes did not differ in the orientation strategies that they exhibited. Once released, we found (unsurprisingly) that pheasants generally preferred to occupy woodland and avoided open habitat. Male pheasants were more likely to use open habitat than females and females showed a stronger preference for woodland than males, replicating previous findings by Hill and Ridley (1987). Female pheasants also actively avoided urban habitat whereas male pheasants did not. The strategy that birds used to solve the maze task did not impact on the use of woodland or open habitats. However, birds that used an allocentric strategy were more likely to use urban habitats. Therefore, the orientation strategy exhibited by an individual early in its life predicted, to some extent, how it would preferentially occupy certain habitats later in life when moving in the wild and thus shaped the spatial ecology of animals at an individual level.

Despite being reared under apparently identical conditions, we show that individual pheasants utilise different orientation strategies when solving a maze task. This extends the work of Alves et al. (2007) who found differences in orientation strategies between individual cuttlefish. However, whereas Alves et al. (2007) used wild-caught individuals (trawled from the English Channel), the differential experience of salient spatial cues within their former habitat was

unknown. While we cannot exclude the explanation that very subtle differences in experience may have led to the differential use of spatial cues in pheasant chicks, our efforts to ensure uniform rearing conditions from hatching make it likely that other factors, for example genetic differences, may influence inherent preferences in attention to cue types.

An individual's orientation strategy had a strong influence on their pattern of preference for urban habitats. Although we found no interaction between sex and orientation strategy, sex was also an important factor in patterns of preference for urban habitats. Female pheasants generally avoided urban habitats which matches previous studies that have found sex differences in response to human disturbance (Saïd, Tolon, Brandt, & Baubet, 2012). Males may be more likely than females to occupy 'riskier' but nutrient rich habitats to maximise their competitive advantage (Prins, 1989). Within sexes, females that used either a mixed or egocentric strategy in the maze task were found to be more averse to urban habitats compared to females that used an allocentric strategy. Similarly, although in general male pheasants had a lesser aversion to urban environments than females, those that used a mixed or egocentric strategy in the maze task also used the urban habitat less than those that used an allocentric strategy. The urban habitats in our study consisted of agricultural buildings, yards and rural properties and gardens which provided stable, conspicuous visual landmarks that could be used as reliable distal cues. Man-made structures provide particularly stable and salient landmarks which would make navigation using allocentric cues an effective strategy (e.g. in homing pigeons, *Columba livia domestica,* Mora, Ross, Gorsevski, Chowdhury, & Bingman, 2012). This finding matches previous work that has shown differences in strategy use between species (Bruck et al.,

2017) and populations (Odling-Smee & Braithwaite, 2003) to be related to differing availability of cues within the places they inhabit. In contrast to previous work, in this study we performed the assessment of orientation strategy before the individuals had encountered any of the available habitat. This leads us to conclude that inherent preferences for a particular spatial orientation strategy may influence the use of habitats, rather than vice versa. However, it is important to note that other factors could also play a role in this behaviour. For instance, in figure 6.6 there are potential additional groupings of raw data that have not been explained by differences in sex or task performance. Bold-shy personality types have also been found to play a role in habitat use (Bonnot et al., 2018) and influence orientation strategy (White et al., 2017) therefore, future work should attempt to include personality within the measures of individual differences.

Sex, but not orientation strategy, predicted the use of woodland (which we expected egocentric individuals to prefer) and open habitats (which we expected allocentric individuals to prefer). While all pheasants preferred woodland habitat above others, females had a higher selection ratio than males, matching previous research on pheasant habitat use (Hill & Ridley, 1987). Conversely, all pheasants avoided open habitats and again, females were the more extreme of the sexes, demonstrating lower selection ratios. One reason for this may be that pheasants show distinct patterns of sexual segregation from release until the breeding season (Whiteside et al., 2019). Females form single sex flocks whereas males tend to avoid each other. This grouping of females may drive the more extreme selection ratios that we found for preference of woodland and avoidance of open habitats.

To explain why ‘allocentric individuals’ differ in their use of urban but not open landscapes, it is useful to identify differences between the two habitat types. While both urban and open habitats may be expected to contain clear landmarks with which to navigate, there may have been differences in distributions and types of food availability between the habitats that means particular orientation strategies are more useful in particular circumstances. For instance, agricultural buildings and yards frequently contain rich but clumped resources (a bird feeder, manure heap or a leaking grain store) which must be precisely located in order to exploit them. Conversely, in open farmland, resources are likely to be much more evenly distributed (insects or grains may be found anywhere within a field), such that precise orientation is less beneficial.

One potential caveat to our study is our use of resource selection functions using a minimum convex polygon to calculate the available habitat. Inherent bias is a common problem with many habitat selection studies and can be directly attributed to the method at which availability index is calculated (Avgar, Potts, Lewis, & Boyce, 2016; Northrup, Hooten, Anderson, & Wittemyer, 2013). Our use of a minimum convex polygon may have created a biased sample, perhaps encompassing more open areas into the available range than we may expect, since pheasants often stay near edges of fields or woodland (Robertson, 1997). Kernel density estimates may offer an alternative for use with a resource selection function that would be less bias in this respect however, kernel density estimates have problems with serial autocorrelation in high temporal resolution datasets (Fleming et al., 2015). Alternatively, step selection functions calculate the availability of habitat using movement characteristics of the study species (Fortin et al., 2005) and would be suitable to use with the high temporal resolution of

ATLAS data. With this being said, we believe that the area used to calculate the availability in this study is representative of the area that the birds are likely to use (*personal observations*) and it is also representative of the area that can accurately be monitored by our system (see Chapter 4). We therefore feel that this is a viable representation of the habitat that is both available and able to be monitored.

We expected that birds who were not using an allocentric strategy would prefer woodland habitat, since distal landmarks are unlikely to be available due to decreased distance in visibility. However, we found no influence of orientation strategy on the use of woodland. Our classification of allocentric/egocentric strategy use was based on a maze and probe trail where good performance was predicted by primarily using allocentric cues and being able to ignore the disruption between allocentric and egocentric cues. This means that the strategy of birds that performed worse in the probe trial could not be distinguished between an egocentric or a mixed strategy. Previous studies have found that animals will often utilise both strategies to an extent (Etienne et al., 1998; Etienne, Maurer, & Séguinot, 1996) suggesting that there could be a continuum of allocentric to egocentric encoding, as has been suggested in humans (Marchette et al., 2011). Further research which dissociates the use of allocentric, egocentric and mixed strategies into more specific categories would give a clearer indication how attention to spatial cue types can influence habitat preference. Finally, although the link between orientation strategy and the use of urban habitats is compelling evidence that attention to certain cue types may be a trait that selection can act upon, the repeatability of these orientation strategies has not

yet been tested. This is an important element to ascertain and should be a priority for future research.

An individual's spatial ecology may be determined by fine scale cognitive processes, such as their orientation strategy which devotes differential attention to spatial cue types, in addition to non-cognitive factors, such as sex, which are well understood to explain differences in movement patterns and space use. Previous research indicates that individuals (at species and population level) occupying specific habitats utilised particular cues, likely based on their experience (Bruck et al., 2017; Odling-Smee & Braithwaite, 2003). Critically, we extend this work by determining an individual's orientation strategy before they had experienced a novel environment. This demonstrates that space use by free-living animals may arise from pre-existing individual cognitive biases. Of course, an individuals' orientation strategy may be refined once in a particular habitat according to the availability and salience of landmarks that they encounter, and selection may act strongly on individuals with orientation strategies that are better or worse suited the habitat that they inhabit. It remains unclear whether orientation strategy is a repeatable trait within an individual and whether it is determined by heritable factors or early life experiences which we did not account for. Regardless of these outstanding questions of interest, our work demonstrates that the spatial ecology of individuals, long assumed to have an important but rather complex cognitive dimension (Fagan et al., 2013; Nathan et al., 2008), may be related to individual cognitive biases for attention to salient cues or memory of previous motor patterns that determine critical aspects of their use of landscape.

7 General Discussion

7.1 Introduction

Individual differences in spatial ability have previously been related to a number of fitness proxies (e.g. survival (Maille & Schradin, 2016a; Whiteside, Sage, et al., 2016), mate choice (Shohet & Watt, 2009), mating strategy (Smith et al., 2005) and reproductive investment by males (Shaw et al., 2019) and females (Branch et al., 2019)). However, studies seldom demonstrate the mechanisms by which spatial cognitive ability affects an individual's movement ecology. It is assumed for most cases, that improved spatial cognitive ability enhances an individual's aptitude to move efficiently and safely when navigating to areas of interest (Fagan et al., 2013). Indeed, theoretical models predict that spatial ability could affect movement choices in a number of ways. For instance, home ranges are expected to encompass the area or landscape within which an individual can store information and selectively exploit (Spencer, 2012) and within these, spatial memory should aid in learning and remembering efficient routes, resource sites and risky areas (Benhamou et al., 1990). At larger scales, memory of distant locations has been hypothesised to support long distance migrations (Bracis & Mueller, 2017). Despite these strong predicted links between spatial cognition and movement, few studies have so far empirically addressed the link between spatial ability and movement in real-world landscapes (but see Campbell *et al.* 2018; Bessa Ferreira *et al.* 2019; Shaw *et al.* 2019). Consequently, theoretical considerations of how spatial ability influences movement ecology at the individual level far outweigh empirical evidence.

Establishing the effects of individual differences in spatial ability on patterns of movement is crucial to understanding how natural selection may act upon

cognitive traits (Thornton et al., 2014; Thornton & Lukas, 2012). In this thesis, I explored the consequences of individual differences in spatial cognitive ability on the spatial and temporal aspects of movement and foraging behaviour using the pheasant, *Phasianus colchicus,* as a model system. I measured individual differences in spatial cognitive ability early in life, using a range of assays targeting different aspects of spatial cognition and asked whether these abilities influenced movement and space use at multiple scales later in life, after release into the wild. First, I assessed the influence of spatial ability on aspects of foraging behaviour using a Eulerian approach to infer movement from presence data at fixed sites to better understand their space use. I utilised the pheasant's reliance on supplementary feeding to track foraging bouts at feeders using RFID technology. In **Chapter 2** I explored the use of foraging sites within a fixed, relatively small area (~4000 m^2) and found that spatial ability assessed early in life, using a binary choice small-scale spatial discrimination task, predicted the diversity of foraging sites used by an individual. Specifically, birds who had a higher probability of choosing the correct location on their 80^{th} trial, i.e. who had learned and remembered the location 'better', used a more diverse range of feeder locations. In **Chapter 3**, using the same individuals, I investigated whether daily foraging patterns were influenced by the same measures of spatial cognitive ability. I predicted that birds with better spatial ability would arrive at feeders earlier, either through leaving roost sites earlier and choosing safer routes or simply arriving at foraging locations quicker by using more efficient routes. This was not the case and instead I found that larger birds arrived at feeders earlier. The early morning predation risk that I predicted would be linked to earlier onset of foraging was not evident at my site and instead birds that fed later in the day (and males) had lower survival probabilities.

I then adopted a Lagrangian approach to assess how early life spatial cognitive ability was related to fine-scale movement patterns. This required the deployment of a newly developed reverse-GPS system to record individual paths at high spatial and temporal resolution: ATLAS. Due to the novelty of the system, I assessed the precision, accuracy and coverage at our field site in **Chapter 4** and developed a simple filter that was successful in increasing the accuracy and precision of locations estimates. I found that accuracy was strongly influenced by the location of the tag with respect to the location of receiver stations and the number of receiver stations that detected the tag. Habitat type did not seem to negatively influence the performance of ATLAS, with woodland habitat surprisingly producing the most accurate locations. However, I suggest that this is due to the location of the main woodland area being centrally located and the focus of the release, and therefore receiver stations were positioned specifically to be in good line of sight of this area. Overall, I found the difference between ATLAS and GPS derived position to differ by ~ 40 m, however accuracy and fix rate issues with the GPS that I used, as well as evidence of realistic movement patterns made by tagged free-roaming pheasants, suggest that the accuracy of our system may actually be higher than reported.

I used the ATLAS system to explore two further movement behaviours that were predicted to be influenced by spatial cognitive ability; movement efficiency (speed and straightness of transitory paths) and habitat use. In **Chapter 5**, I explored the effect of spatial ability on the development of movement paths. Using hidden Markov models, I was able to classify pheasant tracks into three behavioural

states: transit, foraging and resting. Transit between foraging or resting sites was predicted to become less tortuous and more quickly travelled with greater experience of an area. In a novel landscape, I found that birds that were more accurate on cognitive tasks made slower paths than inaccurate individuals, but straightness did not vary according to spatial cognitive ability, although all birds slowly increased their straightness of transitory paths. Over time, these accurate individuals increased the speed of their routes in resulting in no differences between pheasants of differing spatial abilities after one month of tracking. Finally, in **Chapter 6**, I investigated the importance of spatial cues used in navigation strategies by individuals. I predicted that increased attention to either egocentric (e.g. self-directed routes) or allocentric (e.g. landmarks) cue types, expressed as a distinct orientation strategy early in life, could influence individual differences in habitat use later in life. After testing pheasant chicks on their use of cue types in a dual strategy maze, I explored the habitat use of these birds once released. I found that all females actively avoided built-up areas such as agricultural yards and buildings, but those that used allocentric cues in the maze task, avoided these habitats to a lesser extent. In males, individuals that used egocentric cues (or a mixture of cues) showed no preference for built-up areas, but males that used allocentric cues showed a preference for these areas. Built-up areas are likely to be rich in conspicuous landmarks which could be one reason that allocentric-biased individuals were less prone to avoiding them. I suggest that inherent individual preferences for certain cue types may be a factor that underlies habitat selection.

In this thesis, I have provided insights into how spatial cognitive ability relates to multiple aspects of movement and foraging ecology. However, these

relationships are complex and require careful consideration. Specifically, performances on variants of cognitive tasks aimed at measuring spatial cognitive ability were not consistent between tasks, nor did they consistently provide predictable relationships with movement patterns. This complexity will be discussed in this chapter as well as potentially limiting and confounding aspects of my experiments.

First, while pheasants provide many advantages as a study system (see Chapter 1), these advantages comprise one side of a trade-off, which limits the generalisability of our experiments and as such, the complex relationships I have detected between spatial ability and movement may only be relevant to this particular and unusual study system (Section 7.2). Second, determining individual spatial cognitive ability is not a trivial task and choices of assays as well as the appropriate assessment of these assays can have profound impacts on the outcomes and interpretations of studies. It may be that my assays of spatial cognition were inefficient and this explains why I did not find predictable relationships between all measures of spatial ability and movement (Section 7.3). Even if my tasks were robust, a lack of understanding of the cognitive traits and relationships between them, such as their cognitive organisation, phenotypic consistency and genetic heritability make it difficult to fully identify exactly which psychological processes tasks are measuring. If they are genuinely only weakly related to one another and there is no single, simple, spatial cognitive domain, then we may actually expect the pattern of relationships between spatial abilities and movement to be highly contingent on the specific cognitive processes being measured (Section 7.4).

Measuring an individual's use of the spatial environment is also fraught with potential errors, introducing noise into my analyses. If the measures of an individual's movement are suboptimal because of methodological issues, then this may explain why the relationships appear complex. Multiple strategies can be employed to attempt to mitigate these errors and the costs and benefits of these strategies will be discussed (Section 7.5). Alternatively, the complex relationships between specific spatial cognitive abilities and specific movement/foraging metrics may be meaningful and reveal that specific aspects of individual movement are controlled by specific and isolated spatial cognitive processes. Although this scenario does not offer a general theory to link cognition and movement, it does offer the simplest situation by which natural selection could act on particular movement and space use behaviours, and in doing so, exert change on the specific cognitive processes that underly them, rather than explaining the general evolution of (spatial) cognition (Section 7.6).

7.2 Are my findings likely to be specific to the unique and unusual study system, the pheasant?

The role of the pheasant as a managed game bird was key in identifying this species as a model for investigating the relationship between spatial cognitive ability and movement ecology (See Chapter 1). However, the pheasant also provides its own unique challenges and limitations that may make the results obtained in this thesis difficult to generalise.

Firstly, I tested pheasants with a limited range of tasks that were originally adapted from cognition studies on caching birds (Sherry, Krebs, & Cowie, 1981;

Shettleworth & Krebs, 1982) and rats (Olton & Samuelson, 1976). I (and co-authors) developed and refined these tasks so as to be more suitable for pheasants as we gained more experience and tested these tasks on individuals. Despite these multi-year iterations on pheasants (e.g. Langley *et al.* 2018; Chapters 2,3,5 & 6) and although similar tasks have been used on a range of species in recent years (e.g. Ashton *et al.* 2018; Shaw *et al.* 2019), testing for individual differences for cognitive abilities is still in its infancy. Few studies have attempted to use batteries of cognitive tasks and even fewer have attempted to measure the same cognitive process with multiple tasks. Although I attempted this, I found discrepancies between performances across tasks that I assumed measured the same trait (Chapter 2). Since I am unsure of the exact cognitive processes and perhaps even to the existence of these processes as described, one should be cautious when attempting to generalise results to other species. Further research should be conducted to assess a greater variety of tasks to create species-specific task batteries which accurately measure spatial cognitive ability. Furthermore, accurate assessments of these abilities should be developed whereby learning speed, memory accuracy and memory duration can each be assessed separately.

An important feature of the pheasant study system is that one-day old chicks can be (and were) reared without parents in laboratory-style conditions. While this controls for important confounding variables such as post-hatching maternal effects and experience, this unnatural rearing environment may also have had unexpected impacts on the development of behaviour. For instance, social interactions are an important factor that shape movement behaviour in many species (Farine et al., 2014; Guttal & Couzin, 2010; King & Cowlishaw, 2009). In

wild pheasants, chicks rely on their mothers to lead them to appropriate feeding areas (Hill, 1985; Hill & Robertson, 1988). Captivity could reduce opportunities for learning about profitable habitat types, prey items and predators (Håkansson & Jensen, 2005; Santilli & Bagliacca, 2019). Indeed, simple modifications to captive rearing environments, such as increased environmental and dietary complexity have been shown to influence diet preference, cognitive abilities and morphology later in life (Whiteside, Sage, et al., 2016). It may therefore be possible that completing cognitively challenging tasks during the rearing period may have had unpredictable effects on the birds and so limits the generalisability of my results to captive-reared pheasants rather than wild individuals.

Utilising a 'semi' domesticated population of pheasants may also limit the comparative aspects of this work. In the UK, adult pheasants are recaptured for breeding after having lived only 8-10 months in a semi-wild environment where food is readily provisioned. Although pheasants are subjected to heavy predation pressure early in life, especially immediately after release (Madden, Hall, et al., 2018), other selection pressures such as starvation and reproductive success are alleviated through game management and breeding programmes (Draycott et al., 1998, 2005). Such management of the post release environment may reduce the amount of 'challenges' the released pheasants will face compared to wild-reared individuals (pheasants or otherwise), which may impact the ways in which my subjects rely on cognition. However, little evidence supports the notion that domestication reduces any aspect of spatial cognitive ability (e.g.in European sea bass, *Dicentrarchus labrax* (Benhaïm, Bégout, Lucas, & Chatain, 2013) or rats *Rattus norvegicus* (Harker & Whishaw, 2002)). Therefore, I argue that pheasant breeding programs are unlikely to negatively impact cognitive traits.

Releasing many individuals into the same, natural habitat simultaneously is a key advantage to this study system, as it allows control of experience and habitat structure. Soft releases are a well-established protocol that helps game birds to acclimatise to their environment and have been demonstrated to improve survival rates of released birds (Liu et al., 2016). However, the provision of highly predictable food sources (feeders) and the presence of an unnaturally high density of conspecifics that individuals can follow to resources could reduce natural cognitive load, leading to a skewed assessment of how differences in cognitive ability might influence movement behaviour, without the appropriate challenges that most wild animals would encounter. In addition, releasing hundreds of prey into a single area can artificially increase predation pressure through attracting mesopredators (for a review see: Roos, Smart, Gibbons, & Wilson, 2018). While I released a very small number of individuals (100-200) compared to commercial game shoots which often release pheasants in their thousands, some of my released pheasants were killed by predators. I estimate that at least one quarter of my released birds were predated within the field site each year based on field signs from corpses that were retrieved in 2017 (n = 50) and 2018 (n = 60). Birds also dispersed away from the field site which was particularly problematic since both RFID and ATLAS monitor a limited area, albeit at different scales. These losses of individuals impacted upon the timescales at which I could monitor pheasant movement. It also meant that my analyses were restricted to a biased subset of birds that remained within the study site. While this may mean that natural population sizes remain on the field site, this dispersal decreases the power of my analysis. Future research could improve on this by monitoring multiple field sites or a much larger area, perhaps by using more receiver stations with the ATLAS system.

7.3 Are my findings likely to be a consequence of weak measures of individual spatial cognition?

Spatial ability can be inferred by using a proxy of performance exhibited across a variety of tasks in which some aspect of location or route predicts reward. It is commonly assumed that similar tasks targeting the same cognitive domain will correlate (van Horik, Langley, Whiteside, & Madden, 2018). However, such correlations may be disrupted by non-cognitive factors, with an individual's performance in such cognitive tasks being confounded by variables such as hunger (Tolman & Honzik, 1930), motivation (van Horik & Madden, 2016), previous experience (Harlow, 1949), stress (Cazakoff, Johnson, & Howland, 2010; van Gerven, Ferguson, & Skelton, 2016) and the salience of cues (Rowe & Healy, 2014). Yet, few studies have assessed either temporal or contextual repeatability in cognitive tasks (Cauchoix et al., 2018). In pheasants, previous work exploring individual repeatability within the same (non-spatial) task has revealed that it is relatively low (although non-random) (Cauchoix et al., 2018) and correlations between different tasks apparently testing the same process (associative learning) are also poor and inconsistent (van Horik, Langley, Whiteside, & Madden, 2018). Clearly, further work is needed to establish robust assays of individual cognitive ability, free from non-cognitive confounds.

In the 2016 field season (**Chapter 2** and **Chapter 3**), I tested 100 pheasant chicks on two different tasks that I designed to target to assess performance of the spatial domain. The first task was a binary choice small scale foraging task, whereby wells that were situated 1 cm apart contained either a mealworm reward or nothing. The second task that I presented to the pheasants was a larger scale

spatial task, where the birds were lured to the centre of the testing chamber and the reward was located in one of four cups situated in each corner. The 'cup task' is a variant of the open maze or Barnes maze (Barnes, 1979), which is a popular method used to measure spatial ability (Ashton et al., 2018; Boogert, Giraldeau, & Lefebvre, 2008; Croston et al., 2016; Isden, Panayi, Dingle, & Madden, 2013; Shaw et al., 2019). I found no relationship between the binary top-bottom task and the cup task, despite predicting that the tasks measured similar cognitive processes, namely the ability to learn and remember a location. While differences in scales between spatial tasks also seems to have been an important factor in other studies (Guigueno et al., 2015; Sauce et al., 2018) this has rarely been studied specifically. Other factors may have contributed to the lack of relationship. The salience of spatial cues (Hébert, Bulla, Vivien, & Agin, 2017) and the type of spatial cue attended to (allocentric or egocentric) may differ between individuals (as demonstrated in **Chapter 6**) and between tasks (Burgess, 2006). The cup task was conducted in the same testing chamber as the maze task in Chapter 6, where birds could use either egocentric and/or allocentric cues. If birds switched between cue type use between the two tasks (binary choice and cup task task) then this may explain why I found low consistency between task performance. Differences between individuals in the orientation strategies used for the same task would likely blur relationships with other spatial tasks and may explain why I did not find a relationship. Secondly, the birds may not have been able to learn the task to a sufficient level (within the number of trials given) to permit an accurate measure of spatial ability. I doubled the number of trials in the subsequent year **Chapter 5** (2017 field season) for a similar task and found a relationship with movement trajectories. This relationship leads me to suspect

that more trials in the 2016 field season would have yielded different results, and that we did not detect spatial learning due to the lower number of trials.

As well as the type of task, it is also important to consider how performance is measured. Careful consideration of the assessment method is important *a priori*, since for many methods performance in tasks must be monitored consistently to inform the experimenter of when to stop testing individuals. Many studies use a criterion approach whereby for example, 8 out of 10 trials must be correct (Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005) or 10 consecutive trials must be completed with no errors (Means, Woodruff, & Isaacson, 1972). The number of trials researchers set as their criterion varies between studies (although most studies aim for > 80% probability of a correct choice) but does not generally change within a study, despite the fact that the number of trials an animal completes changes the probability that the animal will reach criterion by chance. Furthermore, continuing to test individuals on specific tasks when other individuals have already reached criterion has consequences when subjects undergo a battery of cognitive tests, as each individual will differ in prior experience. For these reasons, alongside logistical motivations, I tested individuals on a fixed number of trials which means that sometimes individuals may not reach criterion before the final trial. To avoid removing individuals from the analyses, I assessed spatial cognitive ability using less common methods. For binary choice tasks I used a binary logistic regression to estimate the probability of a correct choice on the final trial (as in Langley *et al.* 2018b), while taking into account the success of past trials. For the maze tasks, I used a reverse criterion approach and measured the number of consecutive zero-error trials that the birds made across a fixed number of trials. This gave a value of spatial

cognitive ability for every individual and informed me how well an individual had learned the task by the end of the trials. While I believe that my choices of analyses reveal a more accurate representation of an animal's performance on a specific task, my approach does not match the majority of the spatial cognition literature and therefore comparisons between studies may be difficult. Furthermore, although the reverse criterion approach assesses accuracy in a task (as does standard criterion assessments), by using the logistic regression for binary tasks, I may probe different facets of spatial cognitive ability than other studies.

7.4 Are my findings likely to be due to a lack of neural or psychological linkage between specific spatial cognition processes?

For selection to act upon spatial cognitive abilities, performance on tasks that probe processes within the spatial domain should be repeatable across time and contexts (Cauchoix et al., 2018) and have some genetic basis (Thornton & Lukas, 2012; Thornton & Wilson, 2015). In **Chapter 1**, I found that performance on two tasks designed to measure spatial cognitive ability over different scales was not repeatable within individuals. This might be due to my own errors in assessing the exact affordances of the tasks, in addition to birds completing fewer trials than necessary to provide a robust measure of individual differences in performance (see Section 7.3). However, there is little evidence from other studies that show clear, consistent performances across tasks even within the same putative cognitive domain. It is largely assumed that tasks aimed at measuring the same domain should show repeatable performances. Considering that performances

on spatial tasks along with neuronal density and hippocampal size (Clayton & Krebs, 1994a; Pravosudov & Roth, 2013; Roth & Pravosudov, 2009), strongly link to an individual's spatial ecology through both home range size (Gaulin et al., 1990) and complexity of habitat they occupy (Lucon-Xiccato & Bisazza, 2017), it would be expected that if these tasks measured the same cognitive processes, they would also be related.

Studies that assess performances across multiple tasks, often do so in an attempt to assay relationships between different cognitive domains, rather than the same domain (Ashton et al., 2018; Isden et al., 2013; van Horik, Langley, Whiteside, Laker, et al., 2018). However, some studies have included in these batteries multiple tasks that largely focus the spatial domain, which load onto factors in the same direction and provide evidence for the existence of a general spatial ability (Galsworthy et al., 2005; Matzel et al., 2003). If selection can act on this trait, then I would expect there to be a heritable component to spatial cognitive ability. However, evidence for the heritability of these traits is relatively sparse and inconclusive (Croston et al., 2015; Galsworthy et al., 2005; Langley, Adams, et al., 2020; Matzel et al., 2003). These inconsistencies may indicate that a general spatial ability may in fact constitute multiple, highly specific spatial cognitive processes that make it difficult to precisely assay. If each task actually assays a specific process, then these may be separately linked to a particular facet of spatial ecology (See Section 7.6). This may be one reason that I did not find a simple relationship between performance on different spatial tasks and my measures of movement and foraging behaviour. Further research is required to categorise cognitive traits through tasks (Rowe & Healy, 2014), before we can categorically assess the heritable basis of cognition (Thornton & Wilson, 2015).

7.5 Are my findings likely to be a consequence of weak measures of individual movement and foraging patterns?

Using a combination of RFID and ATLAS, I attempted to map differences in spatial cognitive abilities onto elements of foraging ecology and movement behaviours respectively.

By using RFID readers to monitor foraging behaviour at feeders I estimated the time, to 1 second accuracy, that pheasants were feeding. However, by using only presence data, I undoubtably missed many other occasions that pheasants were foraging, either simply around the feeder or at completely different unmonitored foraging sites. For pheasants reared in environments with moderate dietary complexity, multiple types of food (such as invertebrates or berries) are available (Whiteside et al., 2015), therefore it is likely that at least some individuals did, at some point, forage at locations other than our feeders. This is an important limitation as in both Chapters 2 and 3 I may be missing information that could have contributed to differences in relationships between spatial cognitive ability and foraging behaviour. For instance, in Chapter 2, where I looked at the diversity of foraging patches, I only considered one specific type of foraging patch. With so many other birds in the release pen during the study period, birds may simply not have been able to gain access to the feeder (and RFID reader) and instead foraged within leaf litter around the feeders or in completely different areas. However, in Chapter 3, I provide strong evidence that feeders are the primary goal of pheasants, as most individuals attend a feeder within 1 hour of civil dawn, therefore I suggest that birds that attend feeders later in the day do so because

they have been excluded at an earlier time. Truthing this assumption, perhaps with direct observations would strengthen this argument.

In Chapter 3 specifically, I predicted that spatial cognitive ability would be related to the time of arrival at feeders because birds with better spatial cognitive ability would be able to travel more quickly to feeders through the use of more efficient (perhaps more direct) routes. I did not find any support for my hypotheses within my study, however, a key limitation is that I was unable to monitor the sleeping sites of each individual for this work which, if known, would enable me to more accurately assess how spatial cognitive ability influences movement (and therefore arrival times) between sleep sites and foraging patches. For example, by knowing the time an individual left their sleeping site I would be able to calculate the time in seconds until they reached the foraging site, which may be a better measure to relate spatial cognitive ability to temporal behaviour. Through using Lagrangian methods of monitoring movement and classifying behaviour as in Chapter 5, it could also be possible to detect the start of movement from a sleeping site combined with the RFID data at foraging sites, as well as behavioural classification to detect foraging in other areas. However, this method was unavailable while I conducted the studies in Chapters 2 and 3 (2016).

The ATLAS system provides an excellent resource for long term studies on entire populations. However, due to the novelty of the system, I experienced technical difficulties that limited my ability to track pheasants over the entire winter period (in 2017, Chapter 5). This meant that I was unable to reliably track the development of particular routes as pheasants explored their novel environment,

gained experience and formed their adult home ranges (the predicted maximum area that an animal can reliably keep updated within memory (Powell & Mitchell, 2012)). Instead, I was only able to monitor movement reliably for a period of one month and this period only began 22 days post-release. Increases in the speed of transit over the month from high accuracy birds may be expected to continue further and tracking over a longer time period would enable me to assess these hypotheses.

The temporal issues of long-term tracking were resolved in my final field season (2018), however, I encountered an unexpected problem with the range of our system during this year. In Chapter 6, while I had added an extra receiver station to expand the range of the study, a hardware issue with two receivers resulted in the clocks not synchronising. This was not picked up upon until the end of the season as it had appeared that the system was localising tags (since 3 receivers were synchronised) and that all receivers were detecting tags (they were). However, the production of localisations only utilised the clock-synchronised receivers, limiting the spatial scale at which the system was monitoring. In Chapter 4 I found that movement outside the perimeter of the receiver stations was more likely to be inaccurate, however through the use of filters I was able to largely reduce the occurrence of false positive localisations. I am therefore confident that locations that were estimated by the system, and that remained after filtering, were not erroneous and that my results were not an artefact of inaccurate location estimations. That being said, being able to assess a larger area would have allowed me to monitor more areas of different habitat, which would have been desirable.

7.6 Are my findings due to highly specific cognitive processes are linked to highly specific behaviours?

Despite the potential limitations covered in previous sections of this chapter, my results provide meaningful assessments of the relationship between spatial cognitive ability and varying aspects of foraging and movement ecology. Specific cognitive processes may govern individual differences in space use that lead to potentially complicated relationships.

Perhaps most importantly, my work indicates that differences in the salience of spatial cue types may, as has been suggested in humans (Marchette et al., 2011), vary at the individual level. Some pheasants may remember features and views of the landscape with which they can navigate, whereas others may be more inclined to navigate using habitual routes. This concept requires further study into the individual-level consistency of cue use in dual-strategy environments, perhaps aided by gaze-tracking technology that monitors visual attention (e.g. Kano *et al.* 2018) and so offering unique insights into differential cue use in natural landscapes. It is particularly relevant to consider individual differentiation in cue attention and use with regards to cognitive tasks. Indeed, if individuals use different cues to learn the same task then we may expect them to learn at different rates. This possibility was not accounted for when considering the influence of performance on a spatial cognitive task on the diversity of feeder use, arrival times at feeders or the efficiency of transitory paths. Individuals utilising different cues, even within the same habitats, could mask clear relationships between movement and cognition.

The links I found between spatial cognitive ability and two particular features of space use: the diversity of foraging sites and the changes in speed of transitory paths over time; suggest that the tasks may have been accurate enough to detect at least some aspect of spatial cognition. If an individual performed poorly on a cognitive task and used different cues or strategies to an individual that performed well, the bird will still have failed to retrieve the reward or taken longer/expended more energy in doing so. Even if birds used different cue types preferentially, the salience of cues in an environment may override any underlying cue-biases. Indeed, all pheasants preferred woodland habitat, where trees may block views to salient distal landmarks. In the real-world, movement can be assessed objectively and in relation to other individuals, therefore cue biases (in some respects) are irrelevant.

Although a scenario where specific cognitive processes have complex relationships with spatial ecology does not offer a general theory to link cognition and movement, it does offer the simplest situation by which natural selection could act on particular movement and space use behaviours, and in so doing exert change on the specific cognitive processes that underly them, rather than explaining the general evolution of (spatial) cognition.

7.7 Final summary

My work has demonstrated for the first time, that (aspects of) an individual's spatial cognitive ability can predict their later space use and movement behaviour in the wild. I demonstrate this across a range of ecological contexts including the

use of a more diverse range of foraging sites, changes in the speed of transit in novel landscapes and the use of certain habitat types therefore providing empirical evidence that supports the assertion that cognition plays a crucial role in the movement decisions of an individual, made by Nathan et al (2008) and Fagan et al (2013). This fills a critical gap in the literature by providing a link between cognitive ability and movement ecology, which in turn, may facilitate a way that natural selection could act upon cognitive abilities. However, it appears that very specific spatial abilities relate to very specific aspects of movement and space use. This means that I cannot infer a single general spatial ability or general movement ecology on which selection may act. Instead, my thesis suggests that selection may act via changes in the costs and benefits of particular facets of an individual's movement ecology and on particular cognitive abilities which I have demonstrated underpin animal movement in the wild.

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